

**WATCHING TREES GROW:  
OBSERVATIONS OF RADIAL TREE GROWTH ACROSS MULTIPLE  
TEMPORAL SCALES IN NORTHERN LABRADOR**

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By

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## ABSTRACT

This research assesses whether a refinement of the temporal resolution of tree-ring data can improve our understanding of the radial growth-climate relationship. Two study sites in Northern Labrador were chosen, one coastal (Nain), and the other inland (Kamestastin). In Nain, microcore samples were taken weekly from the same five white spruce (*Picea glauca*) trees over the 2014 growing season. After cross sections were made and stained, the resulting 10µm thin radii provided a direct view of active ring development. In coastal Labrador, radial growth was initiated during the last week of June 2014, and ceased by August 25<sup>th</sup>.

Circumference band dendrometers were installed on white spruce trees at both the Nain and Kamestastin sites. The dendrometers were used to measure micrometre-scale changes over the 2014 growing season. Analogous records of temperature were collected with equal temporal resolution, from an Environment Canada climate station (#8502800), and via a programmable data logger (UX120-006M, Onset HOBO). Correlation function analysis determined the relationship between daily temperature variables and daily variations in stem size. A strong relationship was found between minimum daily temperature and daily stem size at both sites over the eight week long growing season.

Traditional dendrochronological sampling methods were utilized to retrieve tree cores from white spruce and eastern larch (*Larix laricina*) in Nain and Kamestastin. Site-specific master growth chronologies were created using crossdating and standardization techniques. After establishing long term records of monthly temperature and accumulated growing degree-days (GDD) at both study sites, a linear regression analysis was undertaken to determine the suitability of these two variables as predictors of annual-radial growth. An accumulated June/July GDD index was identified as an overall better predictor of annual ring-width than mean monthly temperature variables in northern Labrador.

Exploring radial growth on an intra-annual scale helped to improve our understanding of the complex radial growth-climate relationship in Labrador. This allows

for a strengthening of tree rings as a proxy climate indicator in remote regions of the northern boreal forest. The findings from this thesis provide the tools necessary to improve upon long-term climate reconstruction and forecasts of boreal forest structure in the face of climate change.



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“The only way to make sense out of change is to plunge into it,  
move with it, and join the dance.” (Alan Watts)

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## LIST OF ABBREVIATIONS

AMS	Average Mean Sensitivity
avg	Average
Chron.	Chronology
CO <sub>2</sub>	Carbon Dioxide
Corr.	Correlation
GDD	Growing Degree-Days
July/Aug GDD	Index of accumulated growing degree-days from July and August
June/July GDD	Index of accumulated growing degree-days from June and July
Kam	Kamestastin
km	Kilometre
max	Maximum
min	Minimum
mm	Millimetre
MSI	Mean Series Interrelation
NAO	North Atlantic Oscillation
RW	Ring Width
temp	Temperature
µm	Micrometre
V	Volt

## CHAPTER 1

### INTRODUCTION

#### *1.1 The Boreal Forest*

The circumpolar boreal forest contains over 1.2 billion hectares of forested land, accounting for 29% of the total forested area on earth, and 73% of the earth's coniferous forests (Kuusela, 1992). The boreal forest can be divided into three climatic zones, maritime, continental, and high continental. The maritime zone receives the largest amount of precipitation, mostly falling in the form of snow, and the winters are comparatively mild (Kuusela, 1992). About a third (30%) of the circumpolar boreal forest is located within North America (Hart and Chen, 2006). Stand assemblages within the boreal forest of North America are fairly diverse and include a few dozen species of trees. In northern areas near treeline, stands become heavily dominated by white spruce (*Picea glauca*), black spruce (*Picea mariana*), and eastern larch (*Larix laricina*) (Hart and Chen, 2006).

One of the last expanses of boreal forest in Canada that remains untouched by human development is found in Labrador, which is over 60% covered in forests and woodlands (Roberts et al., 2006; Finnis and Bell, 2015). The principal mechanism governing Labrador's climate is the nearby Labrador Current (Roberts et al., 2006). It has variable control over the landscape, which is dependent on distance from the Atlantic Ocean, acting as a regulatory water body. Four major climatic zones are proposed to exist within Labrador, that include two continental zones within the interior, one driven by coastal processes nearest the Labrador Sea, and another located in the cold northern tundra (Banfield, 1981). There are also significant correlations between winter conditions (mean temperature and precipitation) in Labrador and the North Atlantic Oscillation (NAO) index, providing yet another example of the offshore controls on the climate of Labrador (Banfield and Jacobs, 1998; Richerol et al., 2014).



## ***1.2 Climate Induced Change in the Boreal Forest***

As the climate continues to change, it is projected (with very high confidence) that there will be exaggerated warming in northern high latitudes when compared to temperate and tropical regions (Finnis, 2013; IPCC, 2013; Finnis and Bell, 2015). It has been suggested that further warming could lead to positive changes to the forest tundra vegetation in the northern boreal (Payette et al., 2001; Gamache and Payette, 2004; Gamache and Payette, 2005). Conifers are expected to take on less stunted growth forms and achieve higher levels of reproductive success (Gamache and Payette, 2004; Gamache and Payette, 2005). Recruitment is expected to increase and allow for trees to colonize the currently bare hilltops, and for treeline to extend further north (Gamache and Payette, 2005).

Conversely, with an increase in temperature also comes an increased incidence of potential fire disturbance throughout the spring and summer months (Payette et al., 2001). According to predictions, fire frequency, area burned, fire season length, and fire severity are all expected to increase in boreal regions due to climate change induced increases in lightning ignitions, fire season length, and fire weather severity (Flannigan and Wagner, 1991; Wotton and Flannigan, 1993; Stocks et al., 1998; Soja et al., 2007). It can take trees hundreds of years to re-colonize an area post-fire, depending on the physical and micro-environmental characteristics of the site in question, and depletion of the seed bank (Arseneault and Payette, 1992; Lavoie and Sirois, 1998; Payette et al., 2001). Site characteristics such as soil moisture, lichen cover and soil chemistry are in turn affected by climate, and are shaped over time by the succession of plant assemblages (Gamache and Payette, 2005; Simmard et al., 2007).

Insect attacks also account for a substantial amount of boreal forest deforestation (Volney and Fleming, 2000; Nealis and Régnière, 2004; Bouchard et al., 2006). Spruce budworm alone accounted for an estimated 9% of the annual average forest loss in Canada (estimates from 1982-1987), and this number rises to 36% if all insects and diseases are considered (Volney and Fleming, 2000). Comparatively, fire is responsible for an estimated 12% of the annual average forest loss in Canada, only slightly higher

than spruce budworm alone (Volney and Fleming, 2000). It is expected that with the onset of warmer climates will come an increased incidence and intensity of insect attacks (Volney and Fleming, 2000), a phenomenon that is now being observed in Canada. Within the period between 1990 and 2005, the five years in which the most forest area was disturbed due to insect attacks, were the five leading up to the end of the record in 2005 (Natural Resources Canada, 2007).

These disturbances are all directly linked with and driven by climate. Any form of disturbance, whether due to insect attacks, wildfire, or otherwise can cause forests to flip from a significant sink for carbon to a significant source. In 1992, Canada's managed forest, about 76% of the total forested area, sequestered over 160 million tonnes of carbon dioxide (CO<sub>2</sub>) (Natural Resources Canada 2007). Three years later, due to an unusually high level of fire disturbance, almost an equivalent amount of CO<sub>2</sub> (about 150 million tonnes) was reemitted to the atmosphere (Natural Resources Canada 2007). Projections suggest that if the recent warming trend were to continue, the land biosphere as a whole could become a strong source of CO<sub>2</sub> by 2050. Models illustrate that it is possible that all of the carbon sequestered by soils and vegetation since 1850 could be re-released into the atmosphere by 2075 in a compounding positive feedback loop (Cox et al. 2000).

### ***1.3 Tree Growth-Climate Relationship***

Dendroclimatology is a method used to study past climates and their influence on tree growth. By statistically matching ring-width chronologies with instrumental climate data, this traditional technique allows for an understanding of the complex links between climate and radial-tree growth (Kaennel and Schweingruber, 1995).

Widescale dendroclimatological studies of trees growing at northern high latitudes highlight the significance of temperature in driving radial growth, as it is a limiting factor. More specifically, temperature during the months of June and July are consistently revealed as significant drivers of radial growth in northern regions throughout the circumpolar boreal forest (Cropper and Fritts, 1981; D'arrigo et al., 1992; Briffa et al., 1994; Kirdyanov et al., 2003; Levanič and Eggertsson, 2008). Due to this

relationship, studies with a spatial component generally find that tree growth responds to climate variably along a latitudinal gradient, latitude being the most geographically widespread natural temperature gradient (Huang et al., 2010; Lloyd et al., 2011).

There have been numerous studies concerning the radial growth of the dominant and co-dominant boreal forest tree species in Labrador (Cropper and Fritts, 1981; D'arrigo et al., 2003; Payette, 2007; Kennedy, 2010; Dumaresq, 2011; Nishimura and Laroque, 2011; Trindade et al., 2011; Kershaw and Laroque, 2012). A few of these studies adopted a systematic gridded sampling approach, providing a foundation for future study by beginning to reveal the spatial dynamics between climate and radial growth across the southern half of Labrador (Dumaresq, 2011; Nishimura, 2009). Kennedy (2010) studied the northern portion of the region, looking at white spruce growth at treeline. Each of these research endeavors helped to piece together the temporal and spatial dynamics of the tree growth-climate relationship throughout Labrador.

While the overarching significant relationship between July temperature and radial growth also holds true in Labrador (Payette, 2007; Kennedy, 2010; Dumaresq, 2011; Nishimura and Laroque, 2011; Trindade et al., 2011; Kershaw and Laroque, 2012), it was found that the variable response of radial growth to climate is driven more by longitude than it is by latitude. As one travels west, away from the coast, the strong positive correlation between July temperature and radial growth weakens while temperature from earlier in the growing season becomes increasingly important in driving radial growth (Payette, 2007; Kennedy, 2010; Dumaresq, 2011; Nishimura and Laroque, 2011). Reoccurring themes of inland versus coastal sites appear throughout these studies since the trend of shifting climatic influence along a longitudinal gradient is mirrored throughout the region (Payette, 2007; Kennedy, 2010; Dumaresq, 2011; Nishimura and Laroque, 2011; Trindade et al., 2011; Kershaw and Laroque, 2012).

#### ***1.4 Methods of Measuring Intra-Annual Tree Growth***

The issue with using only traditional dendroclimatological techniques in assessing the relationship between radial tree growth and climate is that this method produces results with approximately monthly resolution, which is too coarse a time scale to answer

certain questions regarding intra-annual growth characteristics and physiological processes. Tree growth and its response to climate works on a much finer temporal scale and more importantly is not aligned to specific calendar timeframes. The relationship between tree-growth and climate has been found to change throughout the growing season, even within a single month (Antonova and Stasova, 1997; Vaganov et al., 1999; Mäkinen et al., 2003). In fact, for trees growing in harsh or limiting conditions, the period during which radial growth is most sensitive to climate can be restricted to only a few weeks (Vaganov et al., 1999).

Microcoring is a technique that can be used for the study of intra-annual radial growth (Rossi et al., 2006). By using a puncher type tool, small microcores can be removed from a tree stem repeatedly without damaging the tree (Rossi et al. 2006). Microcores are small wood cores, 2mm in diameter, which contain the outermost 15mm of material from the bole (Rossi et al., 2006). Taken at regular intervals throughout the growing season, these samples can provide a direct view of tracheid development through time, from initiation of radial growth with the first earlywood cells emerging from the cambium to the maturation of the last latewood cells in the xylem (Deslauriers et al., 2003a; Deslauriers et al., 2008; Moser et al., 2010). Not only can this technique provide information regarding the phenology of the studied trees, radial growth can be directly measured from these small cores, providing a more refined dataset of radial growth.

Furthermore, band dendrometers can be used to accurately measure (within a few micrometres) the continual radial expansion and contraction of trees over a single day; the temporal resolution in this case is programmable and chosen by the user (Ecomatik, 2014). Due to the fine scale fluctuations in tree width recorded by the band dendrometers, a large portion of the diurnal flux is due to hydration and dehydration of the stem (Mäkinen et al., 2003; Deslauriers et al., 2007; Korpela et al. 2010; Zweifel et al., 2010). Nonetheless, important events such as the onset, length of the growth period, and cessation of radial growth, have been successfully inferred from the continuous record of tree growth provided by band dendrometers (Deslauriers et al., 2007; King, 2009; Korpela et al. 2010). By identifying the exact period of growth, and by isolating the radial growth increment from the water signal (hydration / dehydration of the stem), along with

weather data taken over the same period of time and with equal temporal resolution, one can then identify the important climatic drivers of tree growth (Antonova and Stasova, 1997; Makinen et al., 2003; King, 2009; King et al., 2013). Monitoring tree growth with such resolution allows for an entirely new perspective, from the annual to the diurnal, providing a different understanding of how climate impacts radial growth, and a better understanding of the mechanisms of tree growth and ring development (Antonova and Stasova, 1997; Vaganov et al., 1999; Deslauriers et al., 2003b; Mäkinen et al., 2003; Deslauriers et al., 2007; King et al., 2013).

### **1.5 Study Sites**

Two study sites were chosen for use in this thesis (Figure 1.1), each representative of a distinct radial growth-climate response zone (bioclimatic zone) as identified by previous research in Labrador (Kennedy, 2010; Dumaresq, 2011; Nishimura and Laroque, 2011). The first site is located in Kamestastin, near Mistastin Lake, Labrador (55°56'48.2" N, 63°07'17.3" W), and was chosen to represent the *Subarctic Maritime* growth-climate response zone (Figure 1.2). Kamestastin is found in inland Labrador, about 100 km inland and about half a degree of latitude south of Nain. Based on observed differences in the temperature records from both sites, this site is characterized by more of a high continental climate that is not subject to coastal buffering or direct offshore control. Situated within the boreal-tundra transition, the study site contained a discontinuous forest assemblage dominated primarily by white spruce tree islands with pockets of eastern larch located in wetter, depressed areas across the landscape. Based on sampled trees, the stands age is variable. Due to its discontinuous assemblage and remoteness, this stand is far less vulnerable to natural or anthropogenic disturbance. The oldest tree was over 280 years old, however, average tree age was between 83 – 104 years.

The second study site is located in Nain, Labrador (56°32'06.6" N, 61°43'23.4" W), and was chosen to represent the *Arctic Maritime* growth-climate response zone after a comparison with previously sampled tree line sites in Labrador (Appendix C) (Kennedy, 2010). Nain is found directly adjacent to the nearby Labrador Sea, this site is therefore characterized by a coastal climate that is heavily influenced by offshore

processes. Situated in a shallow valley, the study site contained a continuous forest assemblage comprised of only white spruce and eastern larch. Based on sampled trees, the forest stand is under 100 years old with an average tree age of about 60 – 65 years.

### ***1.6 Summary and Thesis Structure***

The use of band dendrometers and microcoring are newer approaches in the field of dendrochronology that have yet to be attempted in the forests of northern Labrador. These techniques provide a unique perspective of radial growth on a scale that cannot be achieved with the use of traditional dendroclimatological methods. These new methodologies are used to further the understanding of tree growth in the northern boreal forest.

The **purpose** of this thesis is to determine whether a refinement of the temporal resolution of tree-ring data will improve our understanding of the radial growth-climate relationship. The **objectives** are as follows:

1. To identify the onset and cessation of white spruce radial growth during the growing season (Chapter 2).
2. To determine the main climatic factors influencing white spruce radial growth at treeline with sub-monthly temporal resolution (Chapter 3).
3. To assess whether the radial growth-climate relationship differs between inland and coastal study sites (Chapter 3 and Chapter 4).

The three parts to this study, each explore a different modern dendrochronological method. The exploration of these methods in a logical order allows for each method to expand on and complement the next, allowing for the advancement of previous research. Ultimately, this will lead to a deeper understanding of the radial growth-climate relationship by providing new perspectives that carry across multiple temporal scales.

The thesis is presented in a manuscript-style with Chapters 2, 3 and 4 as stand-alone manuscripts. This therefore results in some repetition and overlap because each individual chapter needs to be an entire picture of the three parts of my research. All data collection in the field was conducted by myself, with assistance from my supervisor Dr.

Colin Laroque, as well as Cecilia Jennings, Scott Wood and Victoria Millette. All data were processed in the lab by myself, and each manuscript was written by myself with editorial assistance from my supervisor and committee members.

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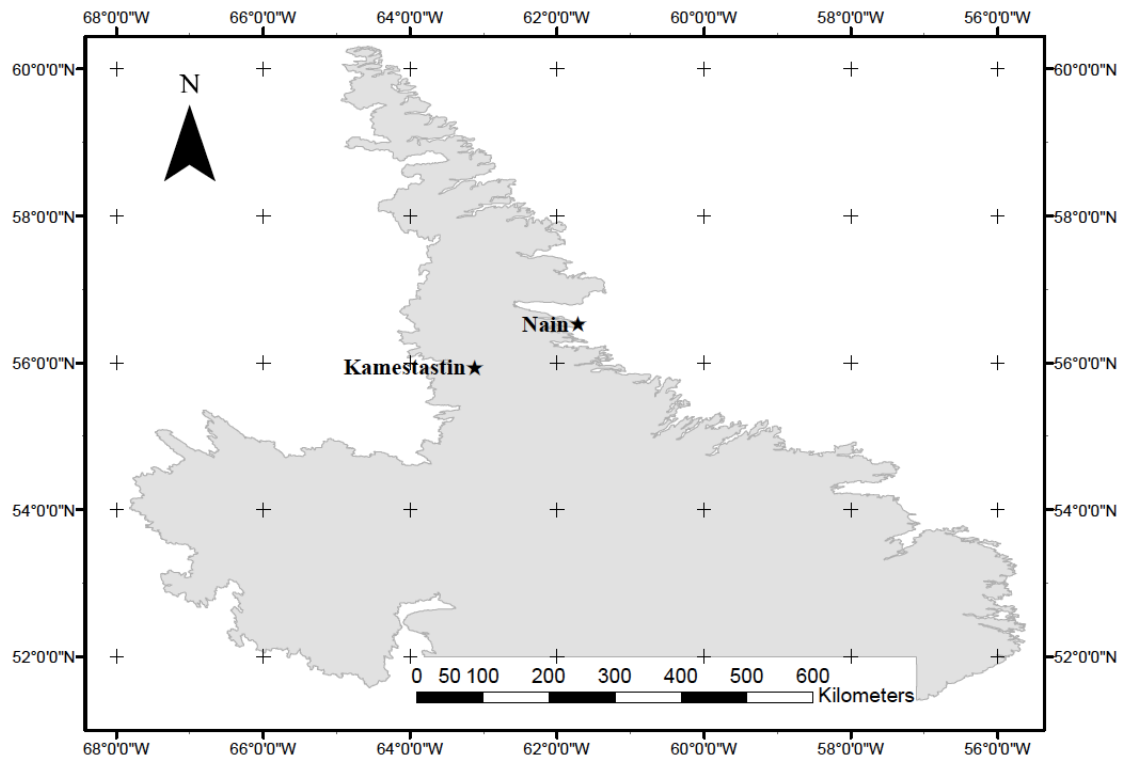
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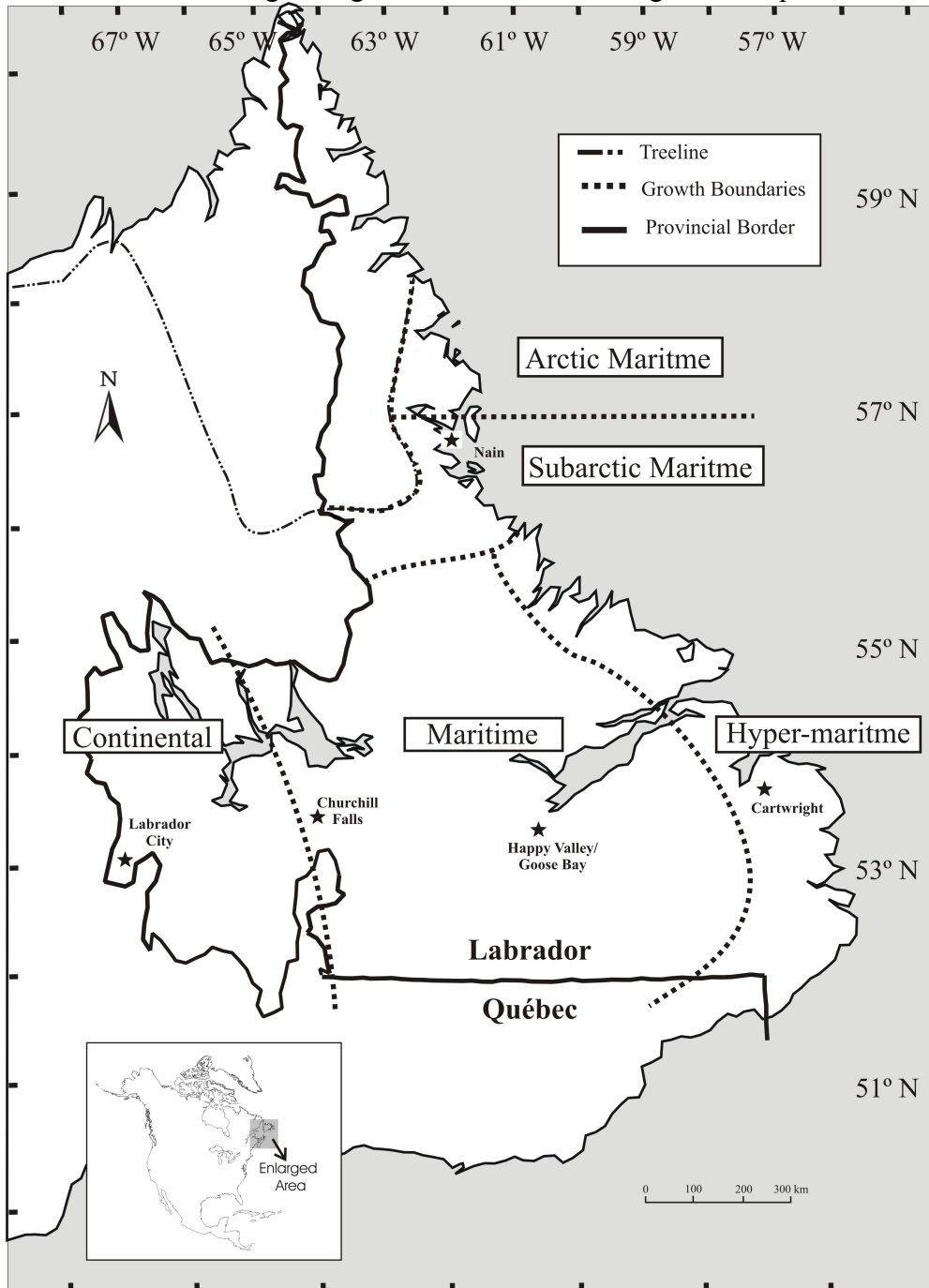
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## 1.8 Figures

**Figure 1.1:** A map showing the location of the two study sites in Northern Labrador, Canada.



**Figure 1.2:** A map of Labrador representing the state of agreed upon biogeoclimatic zones of Labrador prior to this research project (Kennedy, 2010). Based on the findings from the correlation analysis in Appendix C, trees growing within the Nain study site are more related to those growing in the Arctic Maritime growth-response zone.



## CHAPTER 2

### AN ASSESSMENT OF WHITE SPRUCE XYLOGENESIS IN COASTAL LABRADOR

#### *2.1 Abstract*

The phenology of active ring formation in white spruce (*Picea glauca*) growing in coastal Labrador was assessed. Microcore samples were removed weekly from five white spruce trees over the 2014-growing season, providing a direct view of cambial activity and tracheid differentiation. Microcores were thinly sliced on a sliding microtome and stained using two different methods to identify the presence of lignin and aid in the classification of tracheid cells into different stages of development. The approximately eight-week long radial growth season was initiated between June 23<sup>rd</sup> and 30<sup>th</sup> (Julian day 174 – 181) with the first cells emerging from the vascular cambium and entering into their early stages of development. Lignin was first identified within secondary cell walls between July 21<sup>st</sup> and 28<sup>th</sup> (Julian day 202 – 209), signaling the onset of the lignification phase and a near end to the differentiation of the first tracheid cells. A transition to latewood cell production occurred the following week, between July 28<sup>th</sup> and August 4<sup>th</sup> (Julian day 209 – 216). Finally, the end of radial cell production occurred between August 20<sup>th</sup> and 25<sup>th</sup> (Julian day 232 – 237). This is the first study of its kind undertaken in Labrador. New information regarding the process of xylogenesis and the phenology of intra-annual ring development will guide further studies, helping to achieve a deeper understanding of the relationship between climate and white spruce radial-growth in Labrador.

## **2.2 Introduction**

Trees are excellent repositories of environmental information. They respond to the environment in which they reside and internalize a record of past conditions in the form of varying ring-widths (Fritts, 1976). It is common practice to therefore utilize easily obtainable annually-resolved records of radial tree growth to study the environmental and climatic conditions affecting the tree over its lifetime (Schweingruber 1996). This is extremely helpful in areas where the instrumental record is sparse or non-existent, such as in Labrador (D'arrigo et al., 1996; D'arrigo et al., 2003). Here, traditional dendrochronological methods have been utilized to improve our understanding of the radial growth-climate relationship and to further our knowledge of forest ecology and climatology (Cropper and Fritts, 1981; D'arrigo et al., 1992; Briffa et al., 1994; D'arrigo, Cook and Jacoby, 1996; D'arrigo et al., 2003; Payette, 2007; Dumaresq 2011, Kennedy 2011, Nishimura and Laroque 2011, Trindade et al., 2011; Kershaw and Laroque, 2012).

More recently, the benefits of studying intra-annual ring development have been explored (Deslauriers et al., 2007; Zweifel et al., 2010; King et al., 2013; Gärtner et al., 2015). Studying the mechanics of ring development and the phenology of xylem formation can lead to an improved understanding of the climatic controls on ring width (Vaganov et al., 1999; Deslauriers et al., 2003; Mäkinen et al., 2003; Deslauriers et al., 2008). This is especially important for trees growing at high latitudes, where the period of time over which radial growth is most sensitive to climate can be very limited (Vaganov et al., 1999). This type of study has yet to be attempted in the boreal forest of Labrador.

Tracheid cells undergo several stages of development before becoming fully differentiated xylem cells in the active growth ring. Several studies have examined this process in great detail (Fukuda 1996; Samuels et al., 2006; Vavrčík et al., 2008). Newly formed tracheid cells initially go through a stage of radial enlargement where their diameter increases in size, in this phase tracheids have only primary cell walls. The second phase of tracheid differentiation is the wall-thickening phase, in which secondary cell walls are formed. Following wall thickening, later stages of tracheid development begin. Lignin, a structural polymer, is deposited during the end of secondary cell wall



thickening, referred to as the “lignification phase” in this paper. The presence of lignin therefore signals the near end of tracheid differentiation. By this point, tracheid cells have reached their final diameter and wall thickness is no longer increasing. The lignification phase is followed by programmed cell death, after which tracheid cells can be considered fully differentiated (Fukuda 1996; Samuels et al., 2006; Vavrčik et al., 2008).

The primary goal of this paper is to identify the onset and cessation of tracheid cell production in white spruce during the 2014 growing season, thus establishing the main period of white spruce radial growth in coastal Labrador. Beyond this, tracheid cells will be classified into different stages of development and the earlywood-latewood transition will be identified, allowing for a fragmentation of the growing season into distinct stages. This information is needed to improve our understanding of the radial growth-climate relationship. Based on the findings from previous dendroclimatological studies in Labrador (Dumaresq 2011, Kennedy 2011, Nishimura and Laroque 2011, Trindade et al., 2011; Kershaw and Laroque, 2012), it’s hypothesized that the growing season will be relatively short, and limited to the months of June and July.

### **2.3 Study Sites**

A single study site was chosen in concert with representatives from the Nunatsiuvit government and the Nain Research Centre (Figure 2.1). The site represented a common forest type around the town of Nain, Labrador and was in a close enough proximity that local partners could assist with the 12-week long sampling program. The site is located at 56°32’06.6” N, 61°43’23.4” W, and represents the *Arctic Maritime* growth-climate response zone (bioclimatic zone) as defined by Kennedy (2010) (Appendix C). The town site is adjacent to the nearby Labrador Sea, and is characterized by a coastal climate that is heavily influenced by offshore processes. Trees at the site average about 60 – 65 years old, with the entire forest being younger than 100-years old.

### **2.4 Methods**

At the beginning of the 2014 growing-season, five white spruce trees were chosen at random within the Nain study site (Figure 2.1). These trees were tagged and became designated for regular weekly microcore sampling. Small samples were removed using a

punch type Trephor microcore tool (Rossi et al., 2006). This tool produces samples that are approximately 2mm in diameter and contain the outermost material from the stem, the bark, phloem, vascular cambium, active growth ring, and mature xylem from the last few years of growth.

Microcore samples were extracted from the same five white spruce trees weekly from the beginning of June to the end of August 2014. Samples were removed from the stem along a spiral path to avoid sampling damaged tracheid cells from a previous week's punch. Once removed from the stem, the small core samples were immediately placed in a fixative solution (3:1 ethanol:acetic acid) where they remained for 24 hours before being placed in a 70% aqueous ethanol solution and refrigerated for preservation.

Thin cross-sections, about 10 $\mu$ m thick, were produced using a sliding sledge-style microtome in preparation for staining (Gartner et al., 2014). Staining protocols were developed with the purpose of being able to identify the presence of lignin in secondary cell walls. Two thin sections were taken from each core, and two staining methods were developed (Appendix A). The first method was a single staining using 0.1% toluidine blue, and the second, a double staining process, first using safranin O and then secondly fast green (both 0.2%). Utilizing different staining methods on thin sections from the same microcore provided complementary views of the same assemblages of cells. While the double staining method was excellent at showing the presence of lignin (transition from red to brown) (Figure 2.2A), it was sometimes difficult to identify individual latewood cells regardless of their stage of development. Thin sections stained with toluidine blue on the other hand contained latewood cells with defined cell walls that were typically much easier to see (Figure 2.2B). The two staining methods in combination allowed for good visual identification of all types of cells and cell stages within the microcore sections.

The stained sections were examined under a Nikon stereomicroscope with 63X magnification and several measurements were taken from each section. The total number of cells within each of the 2013, 2012, and 2011 rings were counted and recorded by averaging a total of four counts per microcore, taken along two radii from each of the thin sections (see Figure 2.2 A or B). If new xylem cells were present, the total number of

new tracheids was determined by counting cells along a minimum of four radial files within the active growth ring. They were then further categorized into two groups based on the presence or absence of lignin. As mentioned, the lignification of secondary cell walls caused a marked change in their colour after staining, signaling the initiation of later stages of development and the near end of tracheid differentiation. Cells in which lignin was identified were therefore considered as in the “lignification phase”, and those without lignin, were classified as cells undergoing early stages of development.

Cell production differed across samples, due to variations in tree age and ring width along each radii on the stem. To account for this natural variability, a form of standardization similar to that undertaken by Deslauriers et al., (2003) was adopted. A mean was calculated for the 2013, 2012, and 2011 cell counts for each sample along with an overall mean cell count for the same three rings from all weekly samples. The overall mean was then divided by the individual sample mean to achieve a correction factor that was applied to each of the measures of xylem formation taken from an individual sample.

## ***2.5 Results***

The first new tracheid cells were observed in microcore samples taken on June 30<sup>th</sup>, 2014 (Julian Day 181). Figure 2.3 illustrates the progression of tracheid production and development within each of the five sample trees over the 2014 growing season. Due to the variable nature of cell production between trees, standardized cell counts are arbitrary as a comparison measure. All measures of ring width are therefore expressed as a percentage, 100% representing the maximum standardized cell count for that tree by the end of the growing season.

The proportion of cells in their early stages of development peaked on July 28<sup>th</sup> (Julian Day 209) in all but one tree (Tree 171) (Figure 2.4). The maximum proportion of tracheid cells in the early developmental phase at one time was between 28 and 37%. This event coincides with the presence of the first cells in the lignification phase (Figure 2.5). Lignin was first identified within cells present in samples taken 4 weeks after the initiation of xylem cell production, on July 28<sup>th</sup> (Julian Day 209) (Figure 2.5). The

lignification of tracheid cells progressed linearly until the last cell entered this final stage of development.

By illustrating the total proportion of tracheid cells present in the active growth ring regardless of their stage of development, Figure 2.6 is representative of the rate at which new cells are emerging from the vascular cambium over the whole of the growing season. While lignification appears to progress linearly, overall production of tracheid cells accelerates later in the growing season. The rate of cell production was much faster in August than in July. There is also a clear dip in the proportion of standardized cells produced by trees 170 and 173 during the week of July 28<sup>th</sup> to August 4<sup>th</sup> (Julian Day 209 – 216). These trees return to producing cells at a normal rate in the weeks following this aberration. Three of the five sample trees (Tree 171, 173, and 174) also had lower standardized cell counts on August 25<sup>th</sup> (Julian Day 237) than they did five days earlier on August 20<sup>th</sup> (Julian Day 232). This event coincides with the end of cell production for the 2014 growing season.

The proportion of earlywood to latewood varied from 50 – 70% among the five sample trees (Figure 2.7). The transition between earlywood and latewood is very gradual in white spruce making it difficult to identify the exact point at which this transition occurs. For the purpose of this study, the transition was identified where there was a marked reduction in cell size and a clear increase in cell wall thickness. There is also a large difference in the total corrected or standardized cell counts among the sample trees (Figure 2.7). While tree 173 produced only 16 new tracheid cells over the course of the 2014 growing season, tree 170 produced over twice that amount, adding 37 new cells over the same period of time.

The results are summarized in Table 2.1, which describes the phenology of radial stem growth of the sample trees over the 2014 growing season. The temporal resolution of the observational data provided by the microcoring technique is limited only by the microcore sampling interval. For this reason, a one-week range is offered as the commencement of each of the highlighted events except for the cessation of tracheid cell production. Each event represents a stage of tracheid production or development and was initiated synchronously among the sampled trees, at least within the same week. Here the

latewood transition was identified based only on an observed decrease in tracheid cell diameter since newly formed latewood cells have only primary cell walls.

## **2.6 Discussion**

The initiation of tracheid cell production began with the first cells entering the early developmental phase at the end of June. This phase was initiated synchronously amongst the five sample trees with a steep and steady increase in the number of cells entering this stage of development. This increase was immediately followed by a drop in the total proportion of cells in this phase and a period of relative stability, where the number of new cells being created reaches an equilibrium with the number of cells leaving the early developmental phase and entering the lignification phase. When comparing the characteristics of our early developmental phase with that from a similar study by Deslauriers et al., (2003) in Quebec for balsam fir (*Abies balsamea*), it becomes apparent that regardless of the length of the growing season, it takes a similar amount of time for the early developmental phase to reach its apex, signaling the beginning of lignification. This suggests that there is a potential fixed period of time that must pass before the lignification of secondary cell walls in gymnosperms can begin. The lignification phase was also initiated synchronously within the five sample trees and progressed linearly until the end of the growing season.

With only a single year of data collected to date, it is difficult to hypothesize as to why we see an acceleration of tracheid production during the second half of the growing season. This trend is likely climatically driven and would require further investigation regarding the influence of climate on the xylogenesis of white spruce in the region. As for the week of poor cell production at the end of July, while these events appear as a dip on the graphs, they should instead be regarded as simply standstills in radial growth. With as little as 16 – 18 cells added over the entirety of the growing season's annual ring, a single cell can represent over 5% of the growth total for the season. Even if the standardized cell count returns a number only a fraction of a cell lower than that from the previous week it will appear as a significant decrease in standardized cellular growth. Even so, a seven day standstill in tracheid production is in itself an interesting event, perhaps signaling some form of poor climatic conditions, or a physiological switch in the active growth processes

occurring within a tree. Since not all of the sample trees are affected by this week of standstill growing conditions, this could simply be an aberration caused by an abnormally large difference in weekly cell counts due to variations in ring width around the stem.

Rather than identifying the date on which the last tracheid cells reach full maturity or become fully differentiated, what is identified in this paper is the end of radial cell production. At this point, no new cells have been produced, and the lignification of secondary cell walls has begun in all tracheid cells present in the active growth ring. This signals the end of radial growth for the season, as further lignification and programmed cell death will not add further width to the newly formed growth ring (Fukuda 1996; Samuels et al., 2006; Vavrčik et al., 2008). From a dendrochronological perspective, this event is more notable than the moment where tracheids become fully lignified and reach full maturity since it is the final width of the annual-growth ring that is of the most importance. The end of radial cell production occurred in all sample trees between August 20<sup>th</sup> and 25<sup>th</sup> (Julian day 232 and 237). Interestingly, regardless of the differences in cell production between the trees, all major developmental events during the growing season were initiated synchronously among the sample trees, at least within the window of the weekly sampling.

In Figure 2.3 there are clear instances of missing data in trees 171 and 173. Due to the sensitive nature of the vascular cambium at the beginning of the growing season, it was difficult to produce reliable thin sections from microcores taken during the first few weeks of radial growth. Microcores taken from trees 171 and 173 during the week following the initiation of radial growth yielded broken thin sections from which reliable cell counts could not be made. A second microcore taken from tree 173 two weeks later was similarly fragile, again yielding thin sections from which cell counts could not be made. Both of these instances cause a discontinuity in many of the line graphs presented in this paper. While line graphs were chosen as the best way to represent the cell count data, it is important to note that they are not used as a means of interpolating data between sampling instances. They are used only as a tool for visualizing overall tracheid cell development.

## **2.7 Conclusion**

In the 2014 growth year, the eight-week long radial growth season was initiated at the end of June, between June 23<sup>rd</sup> and 30<sup>th</sup> (Julian day 174 – 181). Lignin was first identified three weeks later within secondary cell walls between July 21<sup>st</sup> and 28<sup>th</sup> (Julian day 202 – 209), thus signaling the beginning of the lignification phase. The latewood transition occurred the following week, between July 28<sup>th</sup> and August 4<sup>th</sup> (Julian day 209 – 216), four weeks after cell growth was initiated. Finally, the end of the radial cell production occurred eight weeks after initiation between August 20<sup>th</sup> and 25<sup>th</sup> (Julian day 232 – 237). While our prediction was correct in that the growing season was in fact relatively short, restricted to only eight weeks, radial growth was initiated later than expected in late June and persisted later than expected until the end of August.

This study is the first to examine intra-annual radial tree growth in Labrador. The direct view of tracheid development as provided by the microcoring technique helped amass never before seen details regarding the progression of white spruce xylogenesis in this region and consequently helps to establish the overall radial-growth phenology of white spruce in coastal Labrador. This information will help guide further study and improve our overall understanding of the radial growth-climate relationship.

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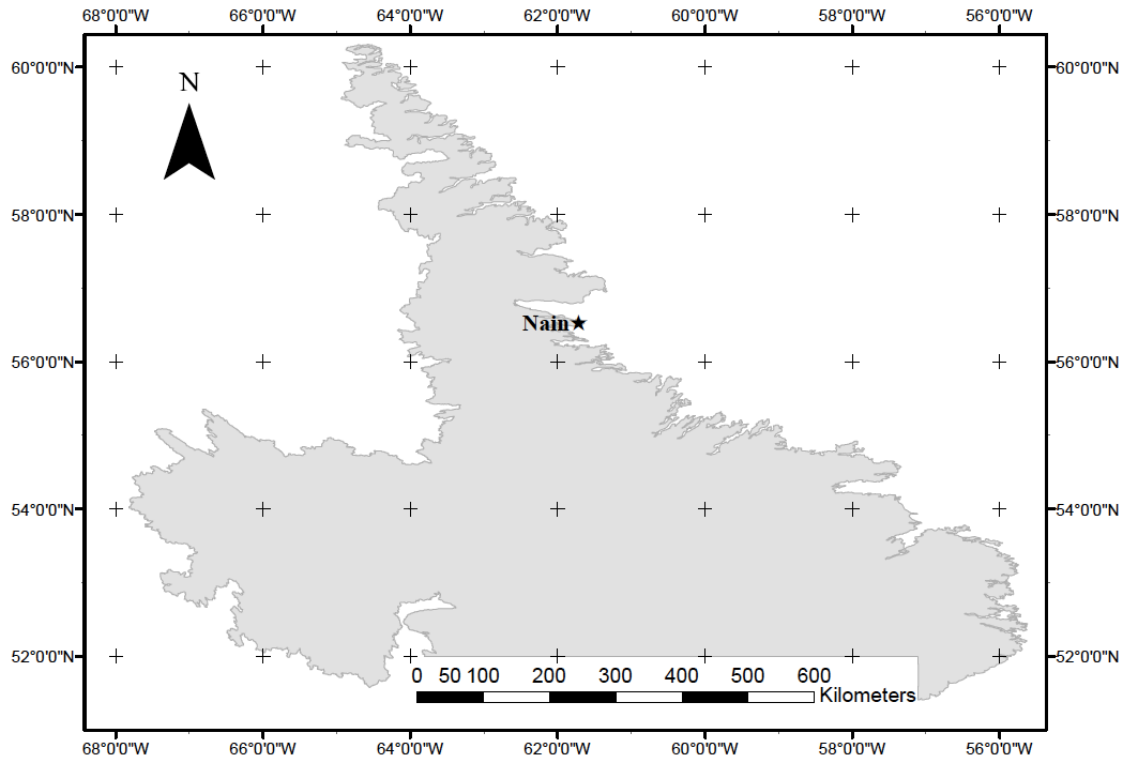
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## 2.9 Tables and Figures

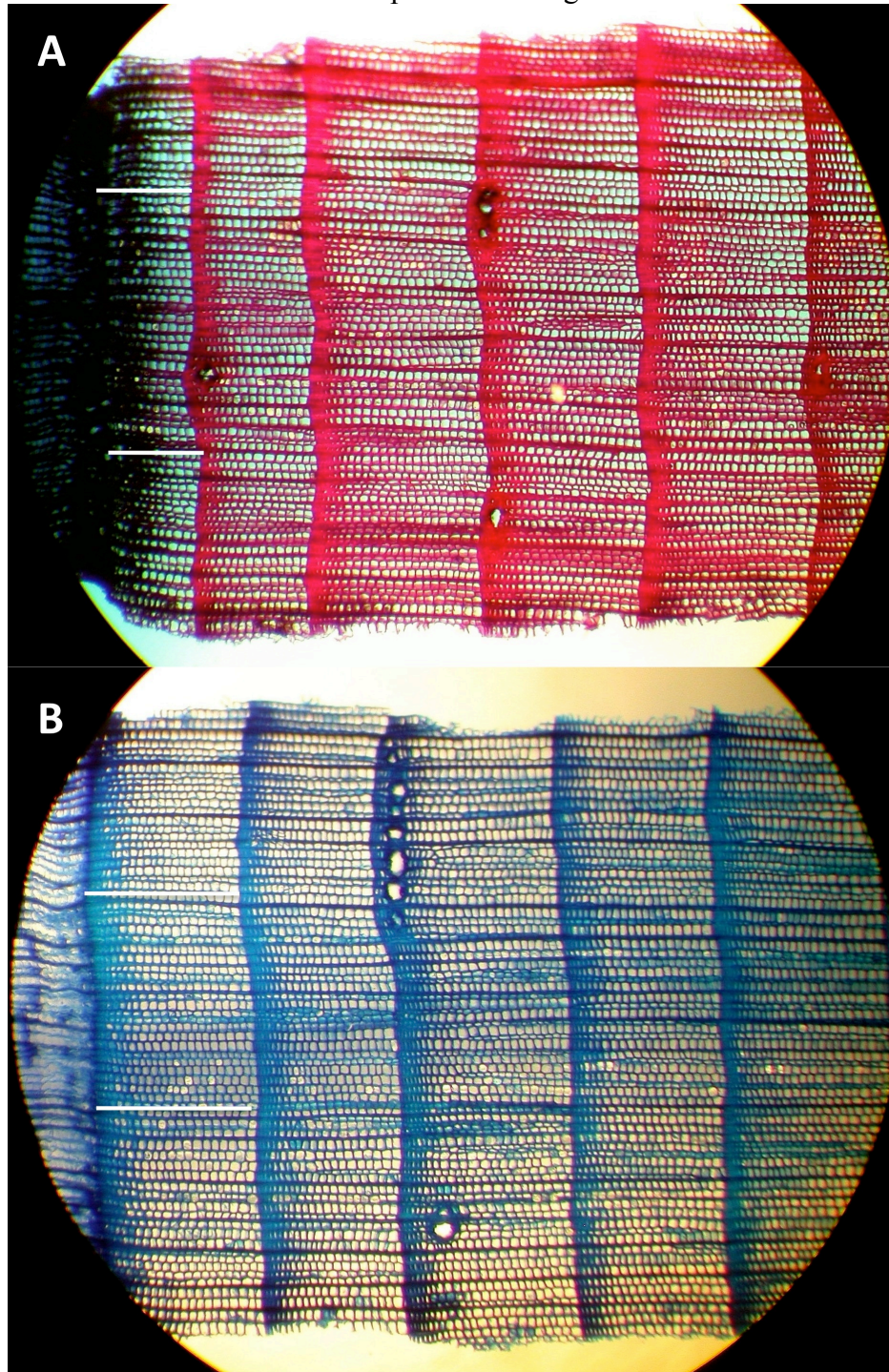
**Table 2.1:** Overall phenology for the 2014 growth ring. The timing for the commencement of each developmental stage is expressed as a range between sampling instances.

Event	Date	Julian Day
Initiation of Radial-Growth	June 23rd - 30th	174 - 181
Lignification Begins	July 21st - 28th	202 - 209
Latewood Transition	July 28th - Aug 4th	209 - 216
End of Radial Cell Production	Aug 20th - 25th	232 - 237

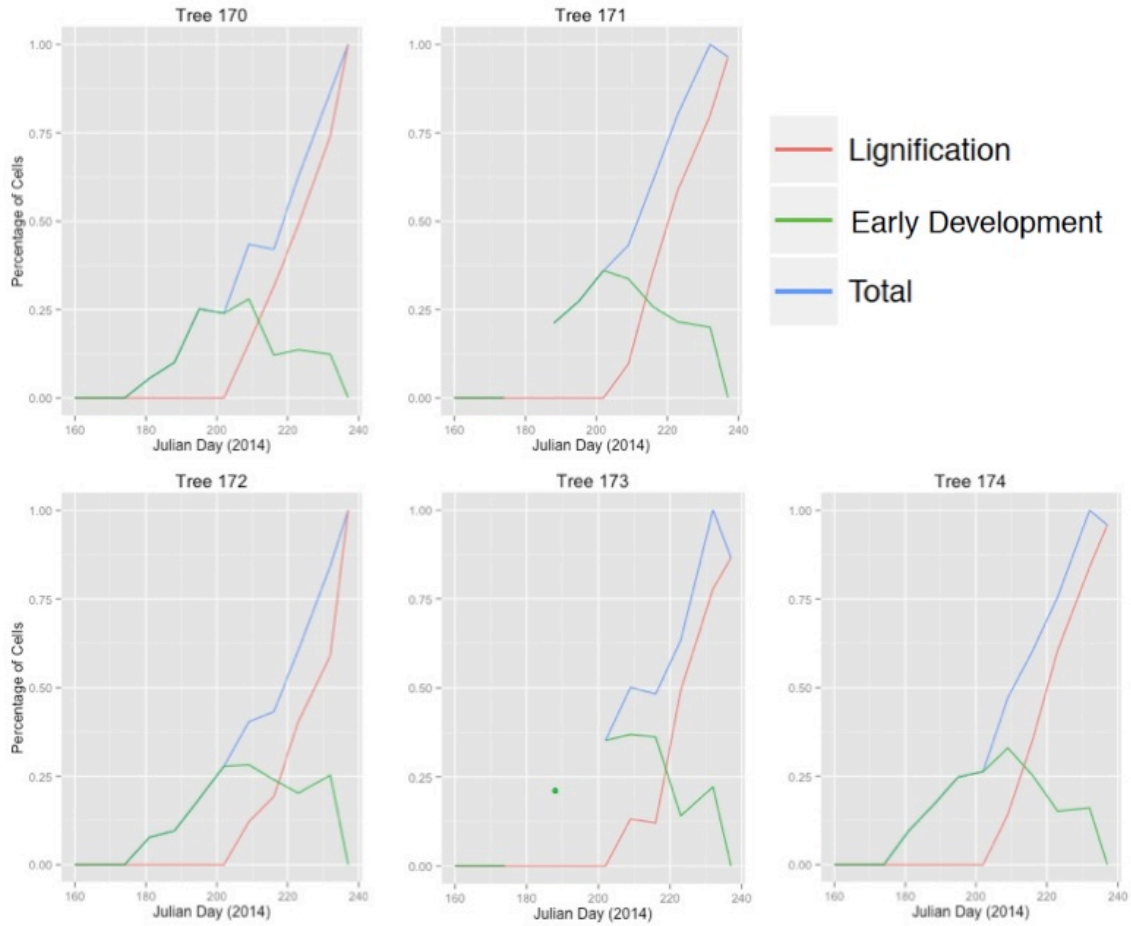
**Figure 2.1:** Location of the Nain study site on the coast of Labrador.



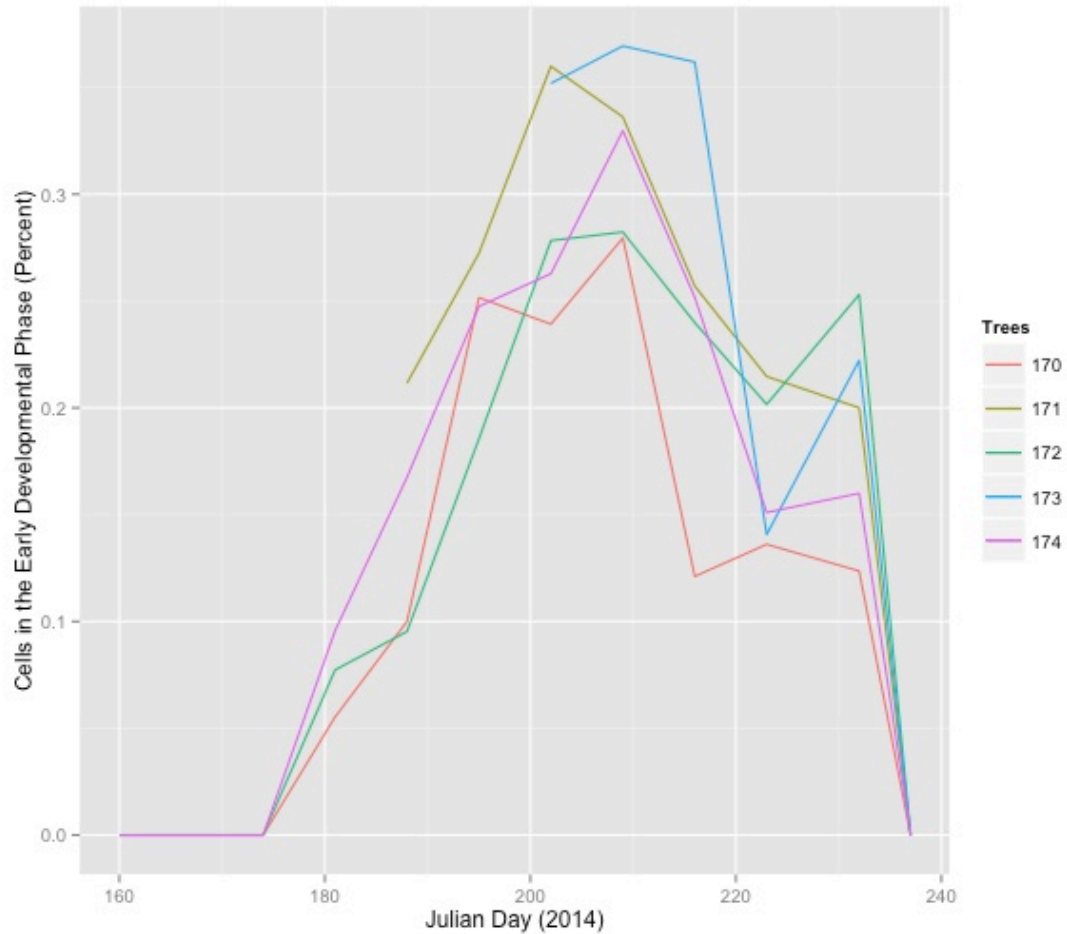
**Figure 2.2:** Photographs of stained thin-sections. The cross section in frame A is from a microcore taken about midway through the growing season, stained using the safranin/fast green double staining method. There is a visible transition from red to dark brown within the active growth ring where the newest tracheid cells have yet to enter the lignification stage. The cross section in frame B is from a microcore taken at the end of the growing season. In this case all tracheid cells have at least entered their final stages of development. The white lines are examples radii along which cell counts could be made.



**Figure 2.3:** The proportion of new tracheid cells in each stage of development at given times over the observation period for each sample tree. The proportions are based on corrected cell counts, 1.00 representing the peak cell count for that tree over the course of the growing season.

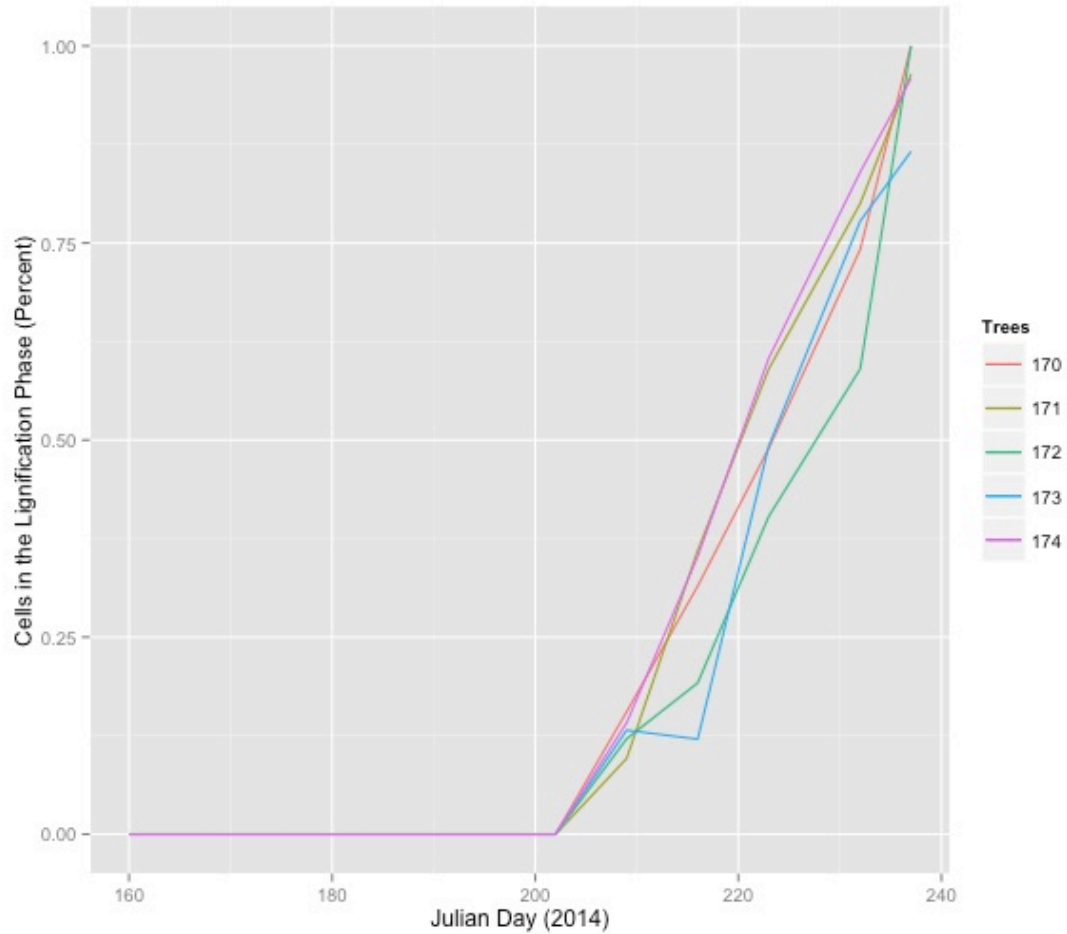


**Figure 2.4:** The proportion of new tracheid cells in the early developmental phase at given times over the observation period, each line representing one of the five sample trees. Proportions are based on corrected cell counts. In this case, no more than 37% (0.37) of the maximum amount of cells produced by a given sample tree is found in this developmental stage at one time.

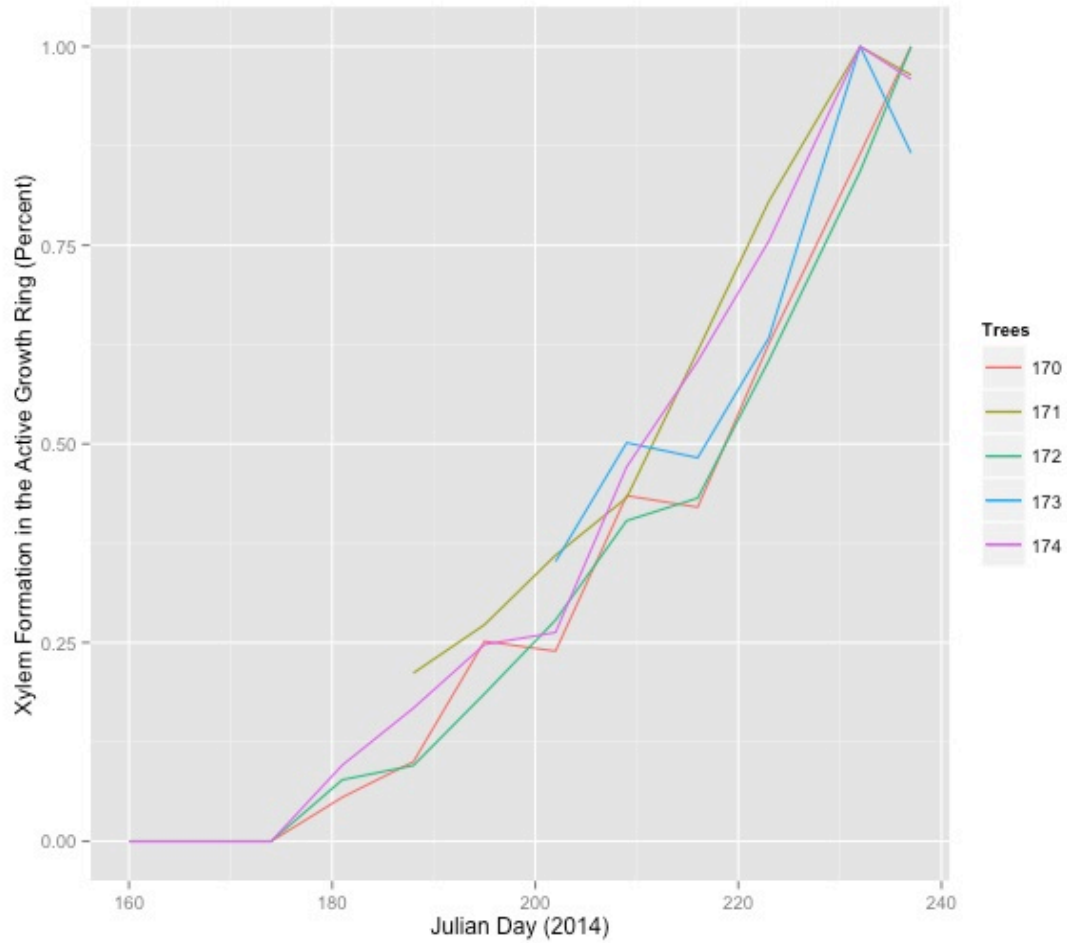




**Figure 2.5:** The proportion of new tracheid cells in the lignification phase at given times over the observation period, each line representing one of the five sample trees. Proportions are based on corrected cell counts, 1.00 representing the peak cell count for that tree over the course of the growing season.

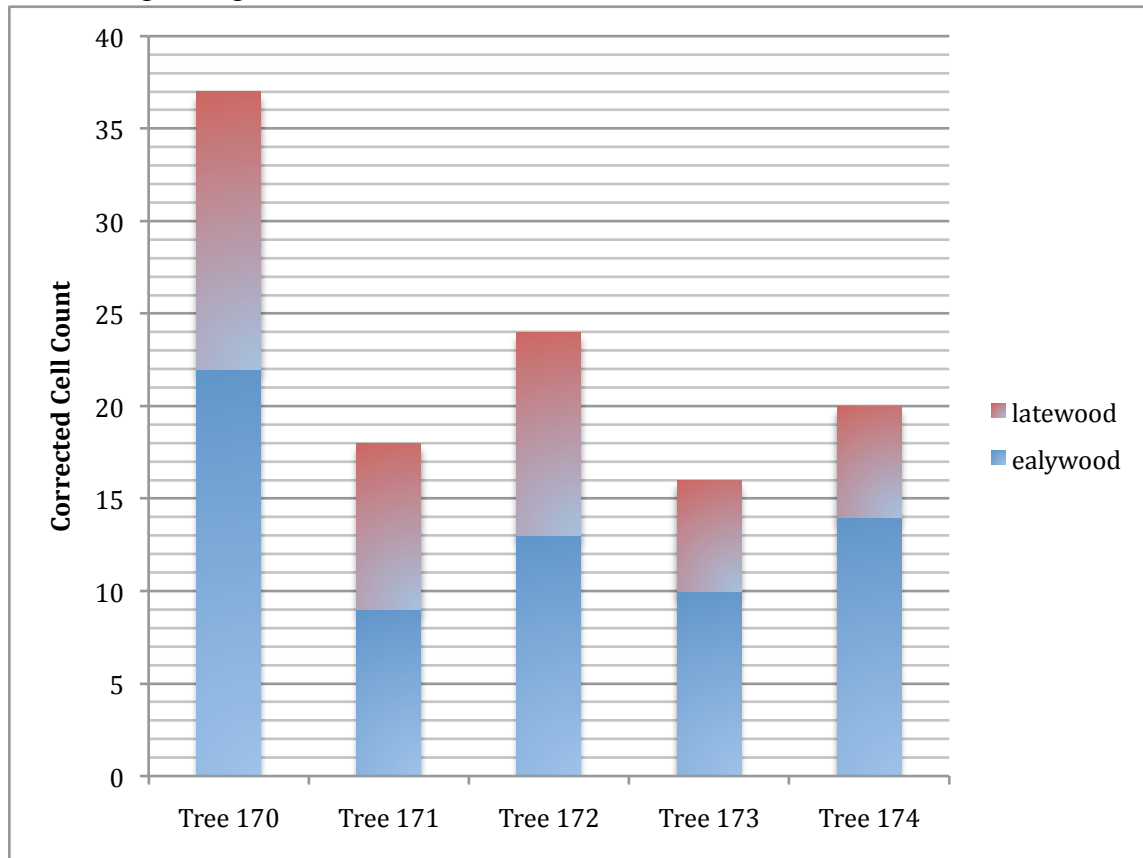


**Figure 2.6:** The proportion of new tracheid cells in the active growth ring regardless of their level of differentiation. Each line represents one of the five sample trees. Proportions are based on corrected cell counts, 1.00 representing the peak cell count for that tree over the course of the growing season.





**Figure 2.7:** A representation of the final earlywood/latewood ratio of the 2014 growth ring, expressed in terms of final corrected cell counts from the last sample taken at the end of the growing season.



## CHAPTER 3

### AN EXPLORATION OF THE INTRA-ANNUAL RADIAL GROWTH-CLIMATE RELATIONSHIP IN COASTAL AND INLAND LABRADOR, CANADA

#### *3.1 Abstract*

The relationship between white spruce (*Picea glauca*) radial growth and climate within the growing season was assessed. Circumference band dendrometers were used to measure fine-scale changes in radial stem size in coastal and inland Labrador over the course of the 2014 growing season. Analogous records of temperature were collected over the same period with equal temporal resolution. DendroClim correlation function analysis was utilized to determine the strength of the relationship between daily temperature variables (mean, maximum and minimum) and daily variations in stem size over the course of the eight-week long growing season.

Minimum daily temperature was a greater predictor of daily radial stem expansion than mean temperature, explaining a maximum of 47% of the variance in white spruce stem size in coastal Labrador. In inland Labrador, minimum daily temperature was also found to be the main driver of change in daily stem size, explaining a maximum of 16% of the variance in white spruce ring-width. The high-resolution records of stem size collected from the two study sites revealed an overall synchronicity over much of the observation period. Divergence in this synchronicity was observed at the beginning and end of the observation period, when the heat capacity of ocean water helped regulate the diurnal temperature range near the coast, causing less suppression in the stem size of trees growing in coastal Labrador when compared with those growing in inland Labrador. The high-resolution records of intra-annual radial growth produced in this study are the first of their kind in Labrador. Monitoring radial-growth over such a fine temporal scale allowed for a deeper understanding of the radial growth-climate relationship, as it functions over a growing season in northern Labrador. This will allow for an improvement of white spruce ring widths as a proxy climate indicator, improving models of past and future climate. It will also allow for a deeper understanding of boreal forest stand structure and tree line dynamics as they shift in the face of further climatic changes.

### ***3.2 Introduction***

The circumpolar boreal forest contains about 1.2 billion hectares of forested land and accounts for 29% of the total forested area on earth (Kuusela, 1992). About a third (30%) of the circumpolar boreal forest is located within North America and much of this is susceptible to anthropogenic deforestation (Hart and Chen, 2006; Natural Resources Canada 2007). While more carbon is currently stored in the boreal forest than in any other terrestrial ecosystem, climatically driven disturbance can cause the boreal forest to flip from a significant sink to a significant source of carbon, an event that is occurring more and more in recent decades (Natural Resources Canada 2007; Carlson et al., 2009). Warming at northern high latitudes is raising concerns regarding the possible impacts of further climate change (IPCC, 2013; Finnis and Bell, 2015). Evidence illustrates that further warming could lead to substantial boreal forest dieback yet much uncertainty remains in these projections (IPCC, 2013). One of the last expanses of boreal forest in Canada that remains untouched by human development can be found in Labrador, which remains over 60% covered by forest (Roberts et al., 2006). Determining the environmental controls on ring width is a necessary step to strengthen the use of tree rings as a proxy for climate reconstructions, especially in remote regions where the instrumental records are quite sparse (D'arrigo et al., 1992; D'arrigo et al., 1996; D'arrigo et al., 2003). This will allow for better forecasting of the change in boreal forest structure due to further climatic changes (Soja et al., 2007).

Until recently, only traditional dendrochronological methods have been used to explore the dynamics of tree growth and its association with climate in Labrador (Cropper and Fritts, 1981; D'arrigo et al., 2003; Payette, 2007; Kennedy, 2010; Dumaresq, 2011; Nishimura and Laroque, 2011; Trindade et al., 2011; Kershaw and Laroque, 2012). Many of these studies have highlighted the overall importance of mean temperature during the months of June and July and provided the first evidence of an observed spatial shift in this relationship along a longitudinal gradient that is mirrored throughout the region (Payette, 2007; Kennedy, 2010; Dumaresq, 2011; Nishimura and Laroque, 2011; Trindade et al., 2011; Kershaw and Laroque, 2012). Reoccurring themes of continentality and the segregation of inland versus coastal sites are found throughout

these studies, yet several unanswered questions remain in regard to the cause of this observed spatial shift.

In the last few decades, several researchers have explored the benefits of studying intra-annual tree growth. It has been found that monitoring radial growth with fine-scale temporal resolution allows for an entirely new perspective that can improve our understanding of the climate-radial growth relationship, and provide better knowledge of the mechanisms of tree growth and ring development (Antonova and Stasova, 1997; Vaganov et al., 1999; Deslauriers et al., 2003; Mäkinen et al., 2003; Deslauriers et al., 2007; King et al., 2013). One of the tools used to monitor fine scale fluctuations in stem size are band dendrometers, which are sensitive enough to measure, within a few micrometres, changes in the radial increment over a single day (Ecomatik, 2014).

The goal of this paper is to explore the relationship between white spruce radial growth and temperature over the course of a single growing season and to assess differences between coastal and inland Labrador. In this study, band dendrometers are used for the first time ever in Labrador to collect records of fine scale variations in stem radius. When coupled with high-resolution instrumental climate data, these near real-time records of tree growth provide an unadulterated observation of the climate-radial growth relationship on a scale not yet examined in Labrador. We hypothesize that there will be an observable difference in the phenology of white spruce radial growth between the two study sites towards a delayed or later growing season (main period of radial growth) in coastal Labrador. Furthermore, we hypothesize that the relationship between temperature and intra-annual radial growth will differ between the two sites.

### **3.3 Study Sites**

Two study sites were chosen, each representative of a distinct radial growth-climate response zone as identified by previous research in Labrador (Kennedy, 2010; Dumaresq, 2011; Nishimura and Laroque, 2011) (Figure 3.1). The first is located in Kamestastin, near Mistastin Lake, Labrador (55°56'48.2" N, 63°07'17.3" W), and was chosen to represent the *Subarctic Maritime* growth-climate response zone (bioclimatic zone) (Kennedy, 2010). Kamestastin is found approximately 100 km inland and about

half a degree of latitude south of Nain. Based on observed differences in the temperature records from both sites, this site is characterized by a high continental climate that is not subject to coastal buffering or direct offshore control. Situated within the boreal-tundra transition, the site contained a discontinuous forest assemblage dominated primarily by white spruce tree islands with pockets of eastern larch located in wetter, depressed areas across the landscape. Based on sampled trees, the stands age is variable. Due to its discontinuous assemblage and remoteness, this stand is far less vulnerable to natural or anthropogenic disturbance. The oldest tree was over 280 years old yet average tree age is between 83 – 104 years.

The second site is located in Nain, Labrador (56°32'06.6" N, 61°43'23.4" W), and was chosen to represent the *Arctic Maritime* growth-climate response zone after a comparison with previously sampled tree line sites in Labrador (Appendix C) (Kennedy, 2010). Nain is found directly adjacent to the nearby Labrador Sea, this site is therefore characterized by a coastal climate that is heavily influenced by offshore processes. Situated in a shallow valley, the study site contained a continuous forest assemblage comprised of only white spruce and eastern larch. Based on sampled trees, the forest stand is under 100 years old with an average tree age of about 60 – 65 years.

### **3.4 Methods**

Circumference band dendrometers (Ecomatik, Type DC2) were affixed to 14 white spruce trees within each of the two study sites, Nain and Kamestastin, in early to mid June of 2014 (Figure 3.1). The dendrometers were used to monitor variations in the radius of white spruce stems over the upcoming growing season. The DC2 type dendrometers are built around a linear potentiometer with an overall plunger range of 15,000µm, over which voltage varies from 0 - 2.5V. A spring provides the necessary tension, pushing the plunger towards the fully extended position, while a metal invar cable, held in a fixed loop around the circumference of the stem, displaces the plunger as the stem shrinks and swells. A measure of plunger position was taken every 30 minutes and was sent to a nearby datalogger (UX120-006M, Onset HOBO) with a resolution of 0.06 µm. The raw measures of the plunger displacement were later converted to a record

of stem radius fluctuations from a universal start point of zero, allowing for a between tree comparison, regardless of initial stem diameter.

Sensor failure occurred at both sites for a variety of reasons (e.g. faulty connection, defective sensors, curious wildlife). Datasets containing missing or false readings were excluded from the study. Within each site, the remaining time series illustrated normally distributed, synchronous variations in stem radius over time, therefore they were averaged to create two site-specific timelines of fine scale radius change. With 30-minute resolution, the timelines are highly variable, containing reversible diurnal fluctuations in stem radius, driven by the daily hydration and dehydration of the stem. To determine the irreversible radial growth increment, a single measure of average daily stem radius and maximum daily stem radius were extracted from each 24-hour day (0:00 to 23:00) of the 82 day record, from both Nain and Kamestastin for the 2014 growing season.

An hourly resolved temperature record spanning the 2014 growth period was extracted from the Environment Canada climate station (#8502800) in Nain. An analogous temperature record was collected in Kamestastin via a programmable data logger (Onset UX 120-006M). Measures of daily minimum, daily maximum, and daily mean temperature were extracted from these temperature records. The long-term Environment Canada climate station in Nain allowed for a comparison of the 2014 temperature record with the 30-year climate normal to assess whether temperature during the 2014 growing season was representative of the norm. Monthly averages for the three daily measures of temperature used in this study (min, max, and mean) were extracted for 2014 and compared against these same parameters from the 30-year period between 1981-2010. Any difference above one standard deviation between the 2014 temperature record and the 30-year climate normal was considered as a significant departure from the norm.

DendroClim2002, a computer program used in dendroclimatological research to run correlation function analysis with bootstrapped confidence intervals (Biondi and Waikul, 2004), was used to assess the relationship between temperature variables and the radial increment on a daily scale. Inputs included time series of the radial increment

(mean and max) and records of temperature (mean, max, and min), both with equal temporal resolution. For the purpose of this study, focus is placed on the relationship between the radial increment and temperature from within the growing season only. The phenology of the 2014-growing season was previously established using a method of regular microcore collection at our coastal study site near Nain, Labrador (Chapter 2). Radial growth was initiated in late June and had ceased by the end of August. This eight-week window therefore became the period of observation. Since there may be a lag in the relationship of these two variables, the temperature datasets were offset by one day at a time from zero to +11. For example, a significant positive relationship between the radial increment and temperature offset by zero would represent a same day positive radial-growth response to elevated temperature. Conversely, a significant positive relationship between the radial increment and minimum temperature offset by +11 would represent an 11-day lag in the positive radial-growth response to elevated temperature.

### ***3.5 Results***

The fine scale fluctuations in average stem size (30-minute resolution) reveal an overall synchronicity in the two records of radius change during much of the observation period (Figure 3.2). Deviations in this pattern occur at the beginning and end of the period, where trees in Nain have consistently larger stem sizes than those growing inland in Kamestastin. The two records become synchronous around Julian day 180 with a relatively uninterrupted increase in stem size at both sites that lasts for several days.

By extracting a single measure of daily stem size from the high-resolution time series, Figure 3.3 and 3.4 show the changes in stem size associated with the daily radial increment. The resulting daily-resolved time series of stem radius change contains less small-scale variability, allowing for a clearer indication of the commencement of certain growth events. The previously observed increase in stem size begins on Julian day 179 and a second period of rapid stem expansion begins on Julian day 202. This second radial growth event lasts several days culminating at a peak stem radius of 0.467 mm and 0.489 mm on Julian day 211 for both records of average and maximum daily stem size respectively.

Comparisons of the 2014 temperature record from Nain against the 30-year temperature normal (1981-2010) reveal that 2014 is representative of a typical growing season (Figure 3.5). October is the only month that consistently illustrates above average temperatures, surpassing one standard deviation in mean, maximum, and minimum daily temperature alike. Beyond this, only one other measure of temperature, the monthly average of maximum daily temperature, differs from the climate normal by over one standard deviation in both March and June. March being colder than normal, and June being warmer than normal.

Several notable characteristics of the relationship between temperature and intra-annual fluctuations in stem size were revealed by the correlation function analysis (Tables 3.1 and 3.2). The relationship between maximum daily temperature and variations in daily stem size was quite weak with both measures of daily stem radius (mean and maximum) from both study sites having few significant correlations (Tables 3.1 and 3.2).

The temperature variable with the strongest correlations is minimum daily temperature, which is significantly and positively related with both mean and maximum daily stem size in both Nain and Kamestastin (Figure 3.6). While minimum daily temperatures affect stem size, this reaction is not instantaneous, lag times exist between these two variables and these differ between the two study sites. These lag times are discussed in terms of a range with a peak, dictated by the amount and level of significant correlations. Minimum temperature exerts its influence on stem size between two and eleven days later with a peak influence at offset +7 in Nain, and between zero and nine days later with a peak influence at offset +2 in Kamestastin, signifying that if an event of elevated minimum daily temperature were to occur, the associated increase in stem size is most likely to occur seven and two days later for Nain and Kamestastin respectively.

A single peak is observed in the range of lag times between the influence of minimum daily temperature on both measures of daily stem size in Nain, this is located on the +7 day offset. The same universal statement cannot be said for the trees growing in Kamestastin. There are two peaks observed in the range of lag times between the influence of minimum daily temperature on mean and maximum daily stem size, they are



located on the two- and seven-day offsets for mean daily stem size, and two- and eight-day offsets for max daily stem size (Figure 3.6). The peak on the +2 offset is more pronounced, returning higher values for correlation in both instances. The influence of mean daily temperature is less important in both Nain and Kamestastin. The significant correlations returned by the correlation function analysis for mean temperature are both weaker and fewer, with a single peak located on the +7 and +4 offsets for both Nain and Kamestastin respectively.

The only significant negative relationship between daily temperature and daily stem size is a negative influence of mean and max daily temperature in Nain, which causes stem contraction with a one-day lag (Table 3.2).

### ***3.6 Discussion***

The correlation function analysis revealed the overall importance of the relationship between minimum daily temperature and daily stem size within the growing season. The difference in the predictive strength of minimum daily temperature varies significantly between the two sites, with the two most important daily temperature variables (mean and min) having stronger relationships at Nain than at Kamestastin. In the Nain study site, daily minimum temperature at its peak influence (offset +7) explains 47% of the variance in the record of mean daily stem size, this is compared with 15% explained by daily mean temperature at its peak influence (offset +7). At Kamestastin when comparing the predictive capability of the same two temperature variables at their peak influence, minimum daily temperature (offset +2) explains 15% of the variance in the record of mean daily stem size while mean daily temperature (offset +4) explains 10%.

Another observed difference between the coastal and inland study sites of Nain and Kamestastin is the divergence in the otherwise synchronous records of stem size at the beginning and end of the observation period. Since temperature is widely accepted as the primary driver of stem size at northern high latitudes (Cropper and Fritts, 1981; D'arrigo et al., 1992; Briffa et al., 1994; Kirilyanov et al., 2003; Levanič and Eggertsson, 2008), one would initially expect that trees growing within the Kamestastin study site

would have a head start with an earlier onset of warm temperatures characteristic of a more continental climate. While mean and max daily temperatures were typically higher in Kamestastin at the beginning of the observation period, our findings suggest that minimum daily temperature is the most important factor driving variations in daily stem size in Labrador. This suggests that there may be a minimum threshold temperature that must be surpassed or maintained in order for radial growth to initiate and progress at a regular rate. While higher day time temperatures are reached in Kamestastin, the nightly minimum is regulated in Nain thanks to the adjacent ocean's capability to store thermal energy (the heat capacity of ocean water) (Figure 3.7) For this same reason, the coastal study site of Nain would retain higher minimum temperatures for longer towards the end of the growing season, explaining the large divergence at the end of the observation period. Higher daily minimum temperatures are probably allowing for a later cessation of growth in coastal Labrador. Because the trees are actively transpiring longer into the late-summer/early-fall period at Nain compared to Kamestastin, trees are able to store more photosynthate during this time for use in the following spring growing period. This pulse of photosynthate energy can also be seen in the apparent divergence of the radial growth record at the beginning of the 2014 season, where the higher amount of stored energy from the end of 2013 allows trees at the Nain site to grow better than at Kamestastin. This divergence persists until both sites warm up and physiological growth processes are once again controlled by the incoming photosynthetic energy levels controlled by the environment, and not the stored sugar reserves.

The steep increase in stem size beginning around Julian day 180 coincides with the increase in minimum daily temperature when growing year environmental controls are once again dominating radial growth (Figure 3.7) and the initiation of tracheid cell production started to occur in Nain during the 2014 growing season (Chapter 2). This rapid increase in stem size occurs synchronously at both study sites, suggesting that perhaps environmental growth control was in fact initiated simultaneously. The second event of rapid stem increase coincides with an observed acceleration of tracheid cell production in white spruce growing near the coast later in the growing season (Chapter 2). This second pulse of rapid stem expansion culminates at a peak, which also happens to coincide with the transition from the production of large earlywood cells to smaller

latewood cells at the Nain study site (Chapter 2). This provides an explanation as to why there is an immediate decrease in the rate of stem expansion following this peak, although this decrease is more pronounced in Kamestastin than it is in Nain (Figures 3.3 and 3.4).

The fact that the 2014 growing season is representative of the temperature pattern over the last 30-year period between 1981-2010 provides confidence in our findings, giving them a quality of longer temporal applicability. The only significant deviations from the climate normal (beyond one standard deviation) occurred outside of the main period of secondary xylem formation, in October.

### ***3.7 Conclusion***

The most significant finding of this study is the importance of minimum daily temperature in driving variations in stem size, and the influence of the tree's proximity to the ocean. Over the years, mean monthly temperature has been primarily used as a universal temperature variable for correlation and response function analysis in dendroclimatological research undertaken in Labrador (Payette, 2007; Kennedy, 2010; Dumaresq, 2011; Nishimura and Laroque, 2011; Trindade et al., 2011; Kershaw and Laroque, 2012). Our findings suggest that further investigation is required to confirm whether mean monthly temperature is in fact the ideal predictor variable. The strong association with minimum temperature on a daily scale suggests that there may be a threshold temperature that must be surpassed for cambial activity to initiate or progress at a regular pace. Such a threshold has been identified at high latitudes in neighboring Quebec (Deslauriers et al., 2008). If this hypothesized threshold temperature was reached later in the growing season, or if minimum daily temperature continuously dipped below this threshold, this would likely be conducive of a less than optimal growing season. It is therefore recommended to investigate the usefulness of growing degree-days or growing degree units, with a base temperature representative of this threshold, as a predictor of radial-growth.

While the observed divergence in the records of radial stem size at the end of the growing season provides evidence of a later end to the growing season in Nain, it appears

as though the initiation of radial growth occurred synchronously between the two sites. We therefore cannot conclusively prove our hypothesis of an overall later growing season in coastal Labrador with these data alone. A more extensive multi-year comparative study using both microcore sampling and band dendrometers in both inland and coastal Labrador would be required to be able to definitively establish a difference in growing season phenology driven by continentality.

Our second hypothesis was in fact validated with the observed difference in the strength of the relationship between minimum daily temperature and daily stem size between the two study sites. While minimum daily temperature was a better predictor of daily stem size in both sites, this relationship was weaker in inland Labrador than it was in trees growing near the coast. This suggests that a universal temperature variable cannot provide equally meaningful results across the whole of Labrador. To further this finding we suggest a large spatial study, utilizing the wide array of sites already sampled in Labrador to compare and contrast the influence of different monthly temperature variables (mean, min, and max), as well as an investigation of the influence of monthly growing degree-days throughout Labrador. This would help in identifying the best variable to use in a given location across the region.

We also suggest the development of an “ideal” variable that better fits the temperature boundaries of the growing season in coastal Labrador. Considering the lag time between our daily temperature variables and radial stem expansion, a predictor variable that fits the period between mid-June and mid-August would likely provide the best representation of this relationship. This could be further broken down into smaller time segments to account for the variable nature of the relationship between temperature and radial growth within the growing season and to determine when climate exerts its strongest influence. It is possible that such a custom variable would be more successful in predicting white spruce radial growth in coastal Labrador than if it were restricted to a traditional calendar month (e.g., June 1<sup>st</sup> to June 30<sup>th</sup>).

Utilizing methods of measuring fine-scale intra-annual radial growth allowed for a deeper understanding of the radial growth-climate relationship in northern Labrador. This information can help to strengthen climate reconstructions that utilize white spruce ring-width as a proxy climate indicator.

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### 3.9 Tables and Figures

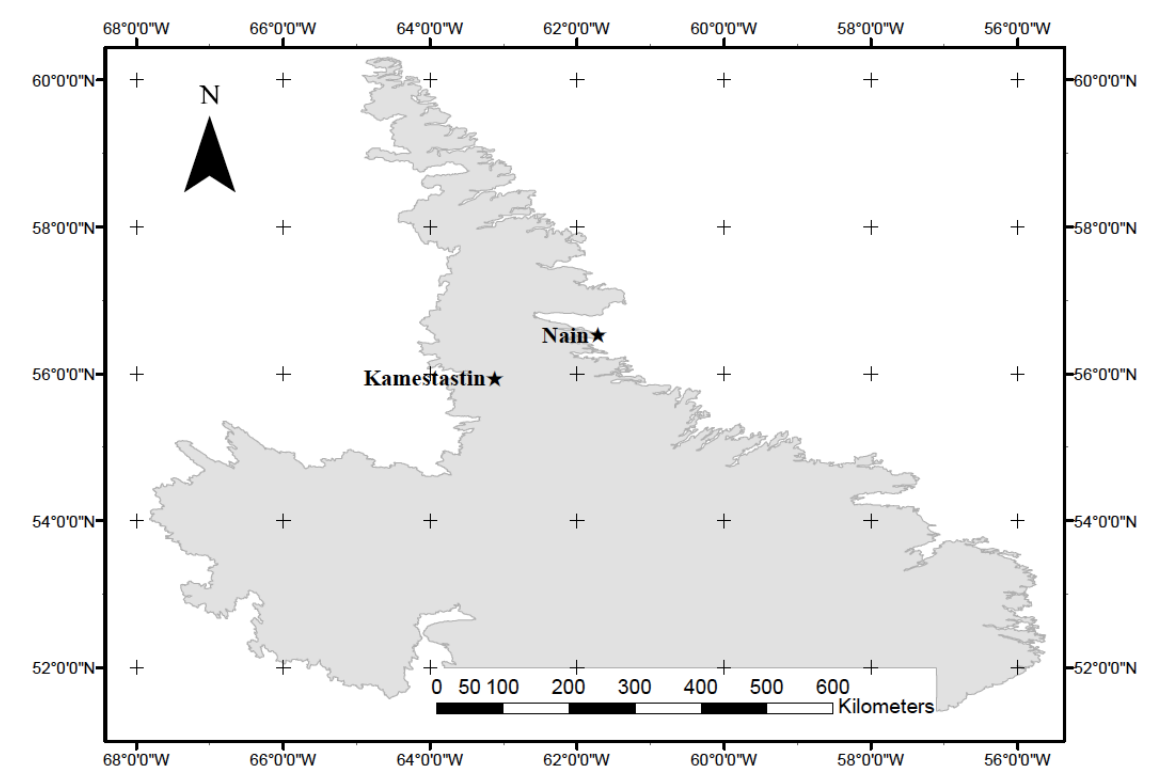
**Table 3.1:** Comparison of mean, maximum, and minimum temperature against records of average daily stem size (top) and maximum daily stem size (bottom) from the Kamestastin study site located in inland Labrador. Each column, 0 to +11 represents an increasing offset between the two variables, 0 representing no offset and +11, an eleven day lag between temperature and stem size. Dark shaded grey cells represent correlations that are above the 95% threshold of a bootstrapped confidence interval.

Kamestastin	Avg	Avg +1	Avg +2	Avg +3	Avg +4	Avg +5	Avg +6	Avg +7	Avg +8	Avg +9	Avg +10	Avg +11
MeanTemp	0.086	0.036	0.155	0.273	0.317	0.256	0.198	0.242	0.196	0.111	0.075	0.056
MaxTemp	-0.062	-0.143	0.020	0.165	0.197	0.134	0.081	0.137	0.086	0.021	-0.055	-0.050
MinTemp	0.320	0.382	0.386	0.379	0.338	0.284	0.275	0.313	0.307	0.263	0.187	0.151
	Max	Max +1	Max +2	Max +3	Max +4	Max +5	Max +6	Max +7	Max +8	Max +9	Max +10	Max +11
MeanTemp	0.108	0.039	0.157	0.285	0.325	0.246	0.194	0.219	0.178	0.110	0.107	0.083
MaxTemp	-0.030	-0.132	0.009	0.180	0.221	0.131	0.078	0.112	0.056	0.021	-0.023	-0.023
MinTemp	0.310	0.368	0.402	0.396	0.326	0.255	0.263	0.322	0.330	0.271	0.208	0.154

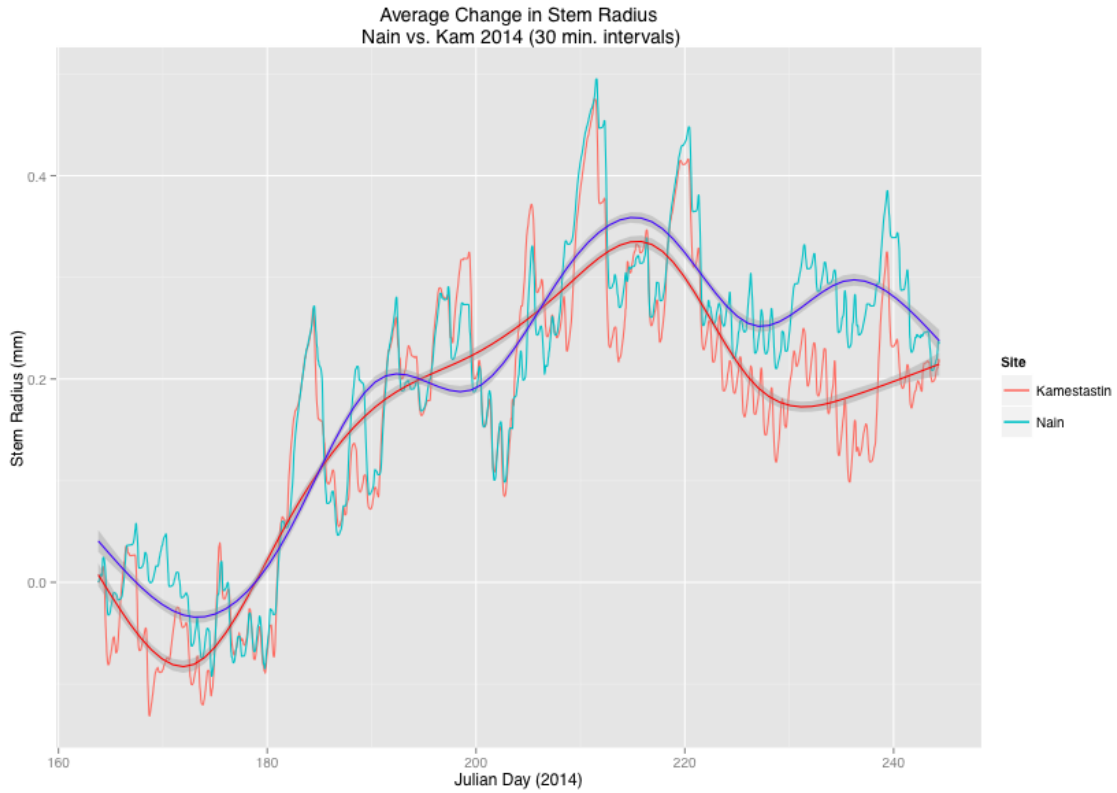
**Table 3.2:** Comparison of mean, maximum, and minimum temperature against records of average daily stem size (top) and maximum daily stem size (bottom) from the Nain study site located in coastal Labrador. Shaded grey cells represent correlations that are above the 95% threshold of a bootstrapped confidence interval.

Nain	Avg	Avg +1	Avg +2	Avg +3	Avg +4	Avg +5	Avg +6	Avg +7	Avg +8	Avg +9	Avg +10	Avg +11
MeanTemp	-0.134	-0.228	-0.022	0.115	0.231	0.319	0.369	0.391	0.290	0.270	0.173	0.060
MaxTemp	-0.160	-0.302	-0.114	0.064	0.199	0.254	0.254	0.277	0.201	0.226	0.170	0.034
MinTemp	0.016	0.039	0.234	0.339	0.399	0.512	0.647	0.687	0.588	0.477	0.341	0.271
	Max	Max +1	Max +2	Max +3	Max +4	Max +5	Max +6	Max +7	Max +8	Max +9	Max +10	Max +11
MeanTemp	-0.081	-0.254	-0.042	0.101	0.214	0.292	0.382	0.382	0.287	0.266	0.195	0.063
MaxTemp	-0.109	-0.320	-0.154	0.055	0.191	0.249	0.252	0.274	0.199	0.211	0.192	0.055
MinTemp	0.019	0.030	0.234	0.319	0.366	0.461	0.647	0.667	0.557	0.467	0.320	0.229

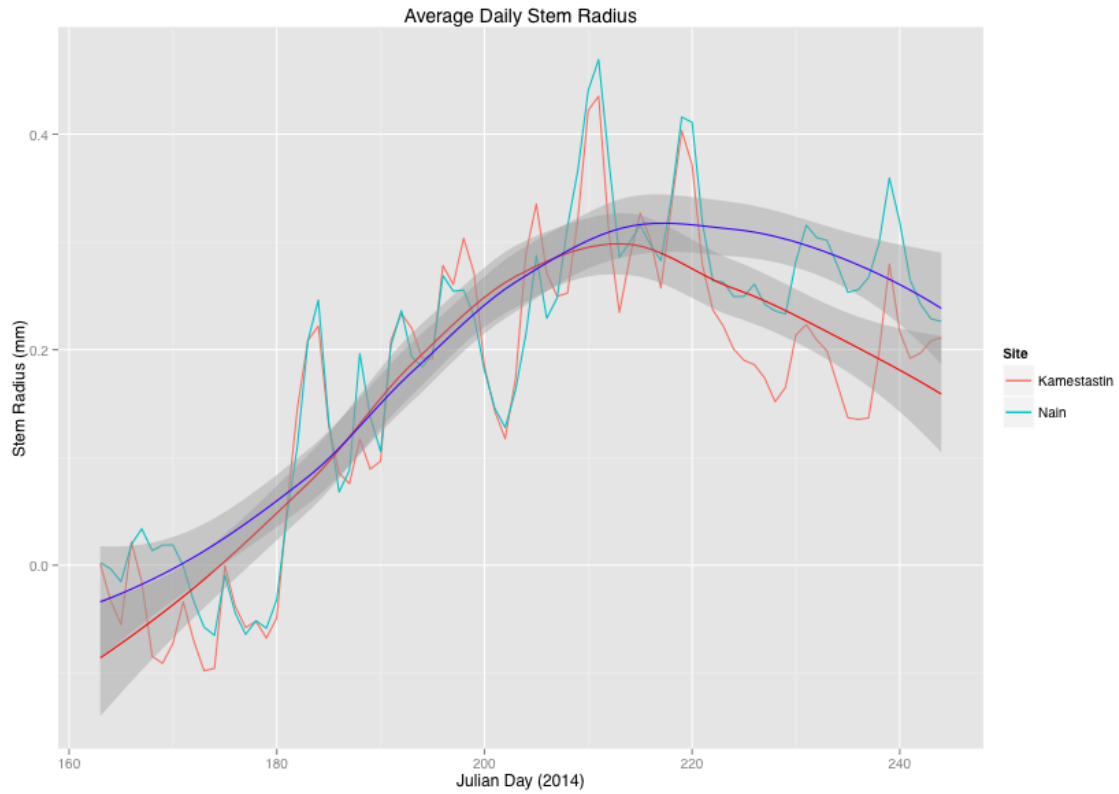
**Figure 3.1:** Location of the two study sites in Northern Labrador, Canada.



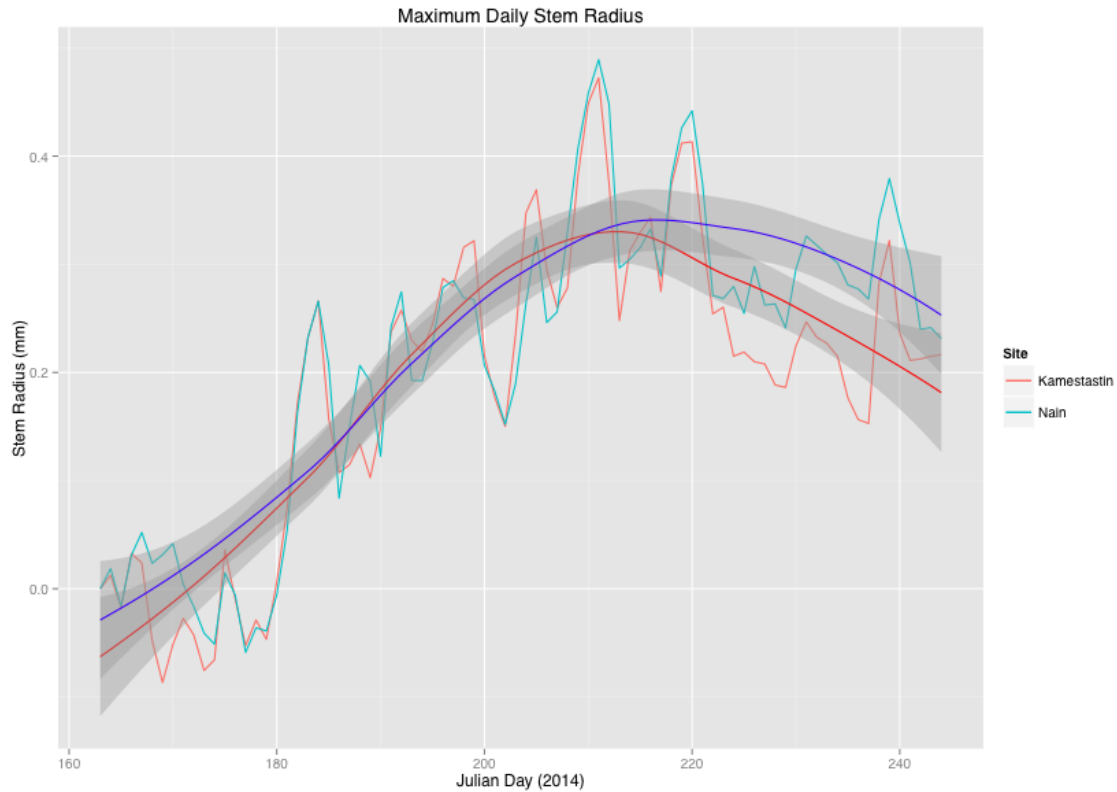
**Figure 3.2:** The raw record of stem radius from both study sites, Kamestastin in red and Nain in blue. Measurements were taken with 30-minute temporal resolution over the observation period between Julian day 163 and 244. The data were smoothed with cubic splines to show the overall pattern of variability. The associated grey shading is representative of the shifting confidence interval.



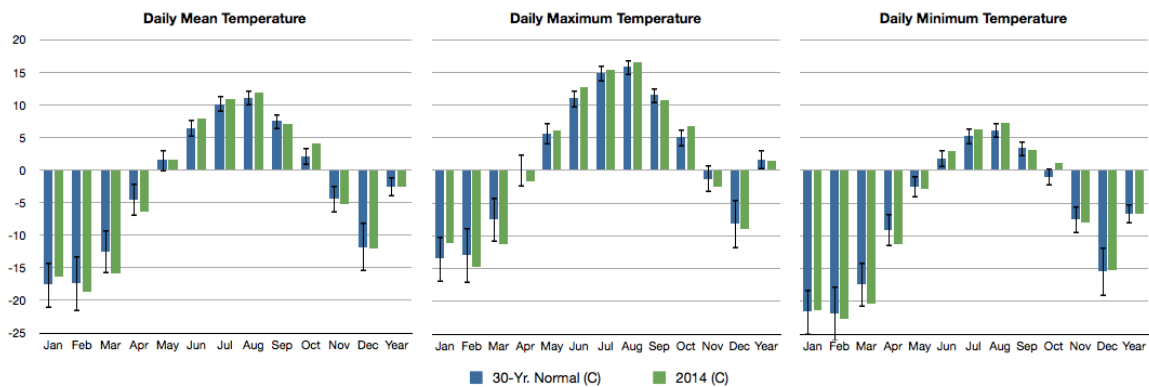
**Figure 3.3:** Average daily stem radius from both of the study sites, Kamestastin in red and Nain in blue. To create these two timeseries, a single measure of average daily stem radius was extracted from each 24-hour day (0:00 to 23:00) within the high-resolution datasets between Julian day 163 and 244. The data were smoothed with cubic splines to illustrate the overall pattern of variability. The associated grey shading is representative of the shifting confidence interval.



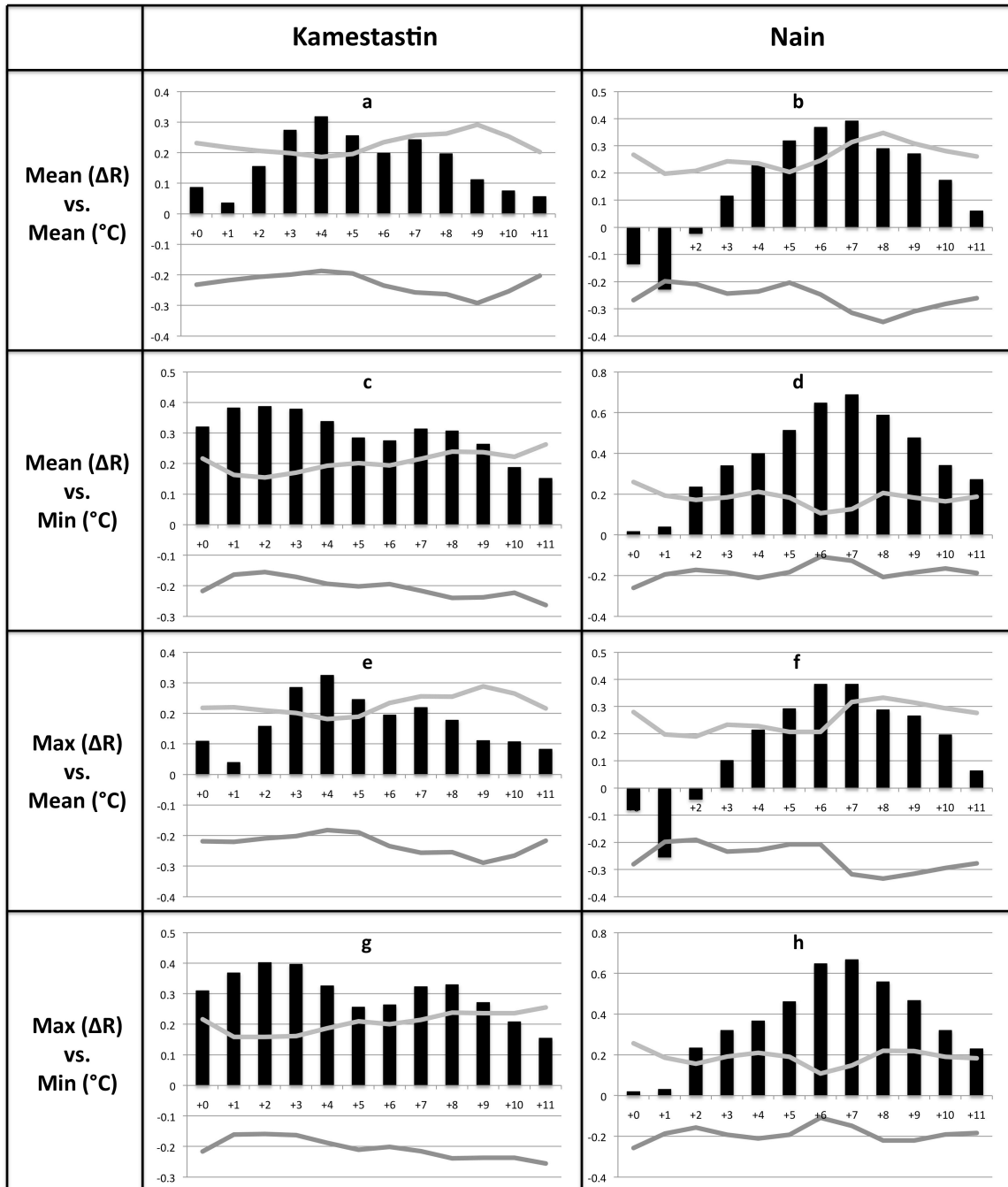
**Figure 3.4:** Maximum daily stem radius from both of the study sites, Kamestastin in red and Nain in blue. To create these two timeseries, a single measure of maximum daily stem radius was extracted from each 24-hour day (0:00 to 23:00) within the high-resolution datasets between Julian day 163 and 244. The data were smoothed with cubic splines to illustrate the overall pattern of variability. The associated grey shading is representative of the shifting confidence interval.



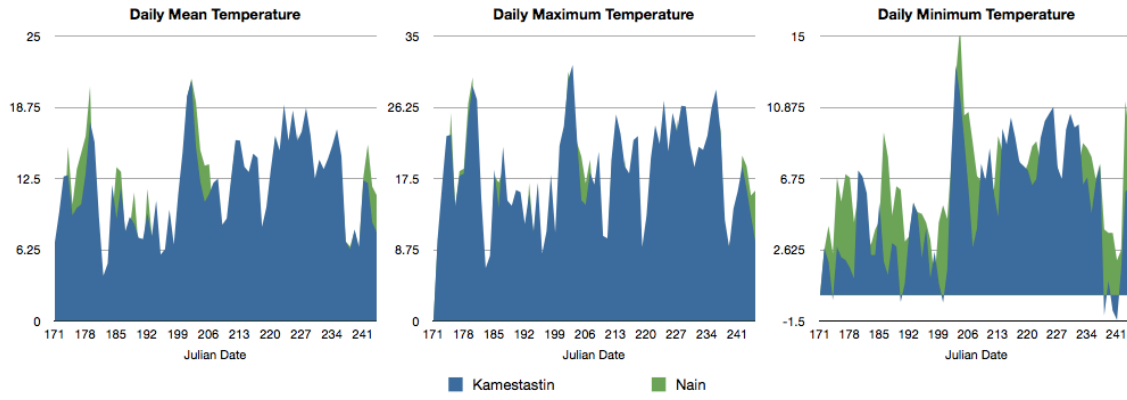
**Figure 3.5:** Comparison between mean, max, and min temperatures in 2014 and the 30-year climate normal, both extracted from the Environment Canada climate station in Nain (Station ID #8502800). Each individual bar is a measure of the monthly mean of each respective temperature variable. The associated error bars represent one standard deviation in the data from the 30-year record.



**Figure 3.6:** Relationship between mean and minimum daily temperature and the two measures of stem size (average and maximum daily stem size). The x-axis represents an increasing offset between the two variables, +0 representing no offset and +11, an eleven-day lag between temperature and stem size. The height of each bar represents the strength of the relationship between the two variables. The grey lines indicate the level of significance needed to surpass the 95% confidence level.  $\Delta R$  refers to the records of daily stem size and is representative of the changes in the daily radial increment.



**Figure 3.7:** A between-site comparison of daily mean, daily maximum, and daily minimum temperature from late-June to the end of August (Julian day 171–244). These overlapping area charts help highlight times over the peak period of influence when a given temperature variable is higher in Nain (green) than it is at the Kamestatin (blue) study site.



## CHAPTER 4

### GROWING DEGREE DAYS AS A PREDICTOR OF RADIAL-TREE GROWTH IN LABRADOR

#### *4.1 Abstract*

The principal drivers of variability in annual ring width were identified for trees growing near treeline in northern Labrador. Forty core samples were removed from 20 white spruce (*Picea glauca*) and 20 eastern larch (*Larix laricina*) trees, two cores per tree, at two high latitude study sites. After establishing long term records of monthly temperature and accumulated growing degree-days (GDD) at the two sites (n= 39 and 59 for Nain and Kamestastin respectively), a linear regression analysis was undertaken to determine the overall strength of these two variables as predictors of annual radial growth.

It was found that a composite variable representing an accumulation of GDD over the months of June and July was a better predictor of variability in radial growth than traditionally used mean monthly temperature variables. Accumulated June/July GDDs explained up to 46.9% of the variability in eastern larch radial growth over the length of the common record. This represents a significant increase in predictive power when compared to that of the linear model constructed using June temperature as a predictor variable. A negative relationship was found between accumulated August GDDs and annual ring width in coastal Labrador. The fitted linear models of ring width as a function of August GDDs in coastal Labrador both had negative slopes and associated  $r^2$  values of 15.8%, and 8.8% for white spruce and eastern larch respectively. Eastern larch was identified as a viable species for future high-latitude dendroclimatological study as this species was very sensitive to environmental inputs and heavily influenced by composite June/July GDDs. The findings from this study can be used to improve upon reconstructions of past climate and better understand the impacts of future climate in the boreal forest of North America.



## **4.2 Introduction**

Previous dendroclimatological research indicates that temperature acts as the main climatic driver of radial tree growth at northern high latitudes throughout the circumpolar boreal forest (Cropper and Fritts, 1981; D'arrigo et al., 1992; Briffa et al., 1994; Kirdyanov et al., 2003; Levanič and Eggertsson, 2008). Due to this strong relationship, the response of radial-growth to climate changes dynamically along a natural latitudinal temperature gradient (Huang et al., 2010; Lloyd et al., 2011). Over the years, much effort has been dedicated to building accurate reconstructions of past climate in the north based on the relationship between monthly temperature variables and variations in tree ring width and density (D'arrigo et al., 1992; Briffa et al., 1994; D'arrigo et al., 1996; D'arrigo et al., 2003; Büntgen et al., 2006; Corona et al., 2010). While the association between temperature and radial growth holds true in northern Labrador, this relationship varies more with longitude than with latitude, an observation that led to deeper questioning in this remote region of northeastern Canada (Kennedy, 2010; Dumaresq, 2011; Nishimura and Laroque, 2011; Trindade et al., 2011). Recent studies regarding intra-annual ring development of white spruce in Labrador have brought into question the suitability of these same monthly temperature variables as an ideal predictor of variability in annual-ring width (Chapters 2 and 3).

Mean monthly temperature is widely used for dendroclimatological study in Labrador (Payette, 2007; Kennedy, 2010; Dumaresq, 2011; Nishimura and Laroque, 2011; Trindade et al., 2011; Kershaw and Laroque, 2012). Recent findings suggest that over the growing season, stem radius is driven primarily by minimum daily temperature, suggesting that radial growth may be strongly threshold driven (Chapter 3). Within a wider context, it has been suggested that treeline coincides with a 6 – 7°C threshold of mean temperature during the growing season (Körner, 2003). More recently, minimum thresholds of mean daily temperature needed for active xylogenesis have been calculated at high altitude in the Alps, 5.6 – 8.5°C (Rossi et al., 2007), and at lower latitudes in Quebec, 8.2 – 9.5°C (Deslauriers et al., 2008). It is very likely that such a threshold exists in the forests of Labrador as well.

Growing degree-days (GDDs) are a metric that measures the amount of accumulated heat over a set time scale (Baskerville and Emin, 1969). A daily GDD value can be calculated by simply subtracting a chosen base temperature value from a measure of mean daily temperature, often expressed as  $((\text{max temp} + \text{min temp}) \div 2) - \text{base temp}$ . The growing degree-days index is seldom used in dendroclimatological research and to the best of our knowledge has yet to be explored as a predictor of radial-growth in Labrador. The goal of this paper is to identify the dominant climatic factors driving annual-radial tree growth in coastal and inland Labrador. With a base temperature set near the minimum threshold for active ring development, we hypothesize that growing degree-days will prove to be a better overall predictor of radial-tree growth than mean monthly temperature in Labrador.

### 4.3 Study Sites

Tree cores were extracted from white spruce (*Picea glauca*) and eastern larch (*Larix laricina*) trees growing within two high latitude boreal forest study sites, one coastal, and one inland. These sites were chosen as representative of a distinct radial growth-climate response zone as identified by previous research in Labrador (Kennedy, 2010; Dumaresq, 2011; Nishimura and Laroque, 2011) (Figure 4.1). The first site is located in Kamestastin, near Mistastin Lake, Labrador (55°56'48.2" N, 63°07'17.3" W), and was chosen to represent the *Subarctic Maritime* growth-climate response zone (Kennedy, 2010). Kamestastin is found in inland Labrador, about 100 km inland and about half a degree of latitude south of Nain. Based on observed differences in the temperature records from both sites, this site is characterized by a high continental climate that is not subject to coastal buffering or direct offshore control. Situated within the boreal-tundra transition, the study site contained a discontinuous forest assemblage dominated primarily by white spruce tree islands with pockets of eastern larch located in wetter, depressed areas across the landscape. Based on sampled trees, the stands age is variable. Due to its discontinuous assemblage and remoteness, this stand is far less vulnerable to natural or anthropogenic disturbance. The oldest tree was over 280 years old yet average tree age is between 83 – 104 years.

The second study site is located in Nain, Labrador (56°32'06.6" N, 61°43'23.4" W), and was chosen to represent the *Arctic Maritime* growth-climate response zone after a comparison with previously sampled tree line sites in Labrador (Appendix C) (Kennedy, 2010). Nain is found directly adjacent to the nearby Labrador Sea, this site is therefore characterized by a coastal climate that is heavily influenced by offshore processes. Situated in a shallow valley, the study site contained a continuous forest assemblage comprised of only white spruce and eastern larch. Based on sampled trees, the forest stand is under 100 years old with an average tree age of about 60 – 65 years.

#### **4.4 Methods**

Two cores were removed from 20 white spruce and 20 eastern larch trees at each site, for a total of 80 cores per site. The coastal site, located in Nain, was sampled at the beginning of the 2013 growing season while trees growing within the inland site in Kamestastin, were sampled the following year, before the beginning of the 2014 radial-growth season. A 5.1 mm increment borer was used to extract cores, which were then stored in plastic drinking straws for transport to the Mistik Askiwin Dendrochronology Lab. Samples were glued to slotted mounting boards before being sanded with progressively finer sandpaper: 80, 120, 220, 320, 400, and 600 grit. The polished nature of the samples helped to reveal cell structure at a microscopic level, allowing for the earlywood-latewood cell boundary to be clear, and accurate measurements to be made. Annual-radial growth was measured using a Velmex stage system under a 63X stereomicroscope, with a precision of 0.001 mm (VoorTech, 2014).

The program COFECHA (Holmes, 1983; Grissino-Mayer, 2001) was used to statistically pattern-match the samples and create an overall intraspecific annual-growth pattern for trees growing within each site. By comparing each core to the overall site-specific master chronology, the program calculates a mean series intercorrelation value, based on overlapping segments. COFECHA flags individual chronologies that are thought to contain errors such as missing or false rings. The measurements are checked and re-checked until there are no remaining flags or until the mean series intercorrelation (MSI) value is well above the threshold for significance at the 99% confidence level (0.4225 using 30-year segments) (Grissino-Mayer 2001).

COFECHA also calculates outputs statistics that provide information regarding some of the growth characteristics inherent to each of the studied sets of cores. Mean sensitivity (AMS) is a measure of how responsive the tree is to its surrounding environment. A measure of AMS between 0.10 and 0.19 is considered low, intermediate values range from 0.20 – 0.29, while series that return a value above 0.30 are considered sensitive (Grissino-Mayer 2001). The autocorrelation value provides information about whether a lag may exist in growth; (i.e., a measure of the degree to which the previous year's growing conditions may affect radial growth during the current growing season).

Resulting chronologies were standardized using program ARSTAN (Cook, 1985). A single detrending utilizing a negative exponential curve was used to achieve a standardized series of cores that is left as unchanged as possible, while still eliminating the inherent biological age-related growth trends held within the time series of the cores. Cores from each site were then averaged using ARSTAN's biweight robust averaging techniques to create standardized and averaged time series of radial growth for each species, at each site. ARSTAN outputs three different yet complementary time series of standardized and averaged tree growth, standard, residual, and arstan. For the purpose of this study the residual series was used as it contains a strong common signal associated with synchronous variability related to climatic control (Cook, 1985).

Past studies indicated that temperature is the most important climate parameter driving tree growth in Labrador (Payette, 2007; Kennedy, 2010; Dumaresq, 2011; Nishimura and Laroque, 2011; Trindade et al., 2011; Kershaw and Laroque, 2012). Temperature records are typically retrieved from standard Environment Canada station archives. Due to the scarcity of instrumental climate data in Labrador, and the propensity for most data to be from coastal locations, a regression analysis was undertaken to develop a long-term, 59 year long temperature series for the remote inland region of Kamestastin.

Hourly climate data were collected from July 2013 to June 2014 at Kamestastin using an Onset HOBO micro station data logger (H21-002). This high-resolution data yielded about 700 measurements per month providing a robust data set suitable for a regression analysis. The Schefferville climate station (station #7117825) in neighboring

Quebec was chosen over the nearest climate station, located in Nain, due to the length of the climate record and its representative nature. Schefferville is not affected by direct coastal buffering; the climate station here therefore produces a temperature record that is more representative of what would be observed at Kamestastin. A linear regression analysis determined the relationship between temperatures at the two locations. The R-statistical package was used to plot linear regressions for every month of the year-long record (Appendix B). The resulting 12 regression equations were then used to build two long-term temperature records for Kamestastin, one with a daily and the other with a monthly temporal resolution, both were extrapolated from the historical mean temperature records from Schefferville station. Similar temperature records were also required for Nain and were available in the Environment Canada archives (station # 8502800).

To test the usefulness of growing degree-days as a predictor of radial growth, a long-term record of GDD was calculated for both Nain and Kamestastin (n= 39 and 59 respectively). The established long-term temperature records were first used to calculate a daily value for GDD by simply subtracting the value of a chosen base temperature from the mean. The base temperature chosen in this case was five degrees Celsius based on the observed minimum threshold temperature needed to initiate physiological processes identified by previous researchers (Rossi et al., 2007; Deslauriers et al., 2008; Körner, 2003). Each daily GDD value within a given month was then added together to create an accumulated monthly GDD variable. It has been established that the peak time during which temperature has variable control over radial growth is during the months of June, July, and sometimes later in the growing season in August (Payette, 2007; Kennedy, 2010; Dumaresq, 2011; Nishimura and Laroque, 2011; Trindade et al., 2011; Kershaw and Laroque, 2012; Chapter 3; Appendix C). Accumulated monthly GDD values were therefore calculated for the months of June, July, and August, along with two composite GDD variables for the periods between June 1<sup>st</sup> – July 31<sup>st</sup>, further referred to as June/July GDD, and July 1<sup>st</sup> – August 31<sup>st</sup>, referred to as July/Aug GDD.

A second regression analysis was undertaken; to compare the predictive capability of previously established predictor variables (June and July temp) and our long-term

records of accumulated monthly GDD (June GDD, July GDD, August GDD, June/July GDD, and July/Aug GDD). Each predictor variable was independently regressed against white spruce and eastern larch ring-width chronologies from both study sites respectively.

#### **4.5 Results**

Both the white spruce and eastern larch trees sampled in Kamestastin were much older than those found at the Nain study site, with the oldest being a white spruce tree determined to be 286 years old at breast height. The average age of white spruce trees was 104 years at Kamestastin and 65 years at Nain, while the average age of the eastern larch trees were 83 years and 60 years respectively (Table 4.1). The series intercorrelation r-values were high in all master chronologies, ranging from 0.507 to 0.770. In all cases r-values were well above the value required for statistical significance above the 99% level, yet series intercorrelations did vary slightly across species and sample locations. When comparing the two sample locations, the trees growing at the Nain site seem to have a more uniform growth signal (0.701 and 0.770) across the group of trees than those in Kamestastin (0.507 and 0.686) (Table 4.1). When comparing the two species, eastern larch trees (whether from Nain or Kamestastin) have a stronger degree of commonality in their growth when compared to their white spruce counterparts that are growing in close proximity to each other (Table 4.1). Based on the measure of average mean sensitivity, white spruce is less sensitive to environmental outputs than eastern larch. The values were intermediate to low for the two white spruce chronologies, 0.175 and 0.208, for Nain and Kamestastin respectively (Table 4.1). They were slightly higher, in the intermediate to high range for the eastern larch, 0.255 and 0.301, again for Nain and Kamestastin respectively. Both species examined also appear to be heavily autocorrelated, with values of 0.727 for Nain and 0.793 for white spruce from Kamestastin, while these rates are lower for eastern larch, with values of 0.648 for Nain and 0.589 for Kamestastin (Table 4.1).

The regression analysis associated with white spruce in Nain (Figure 4.2), showed that mean June temperature and mean July temperature were able to explain 4.5% and 9.7% of the variability in white spruce ring width over the length of the common record ( $n = 39$ ). June GDD and the composite June/July GDD explained more of the variance in

the ring width record with respective  $r^2$  values of 6.7% and 10.9%. July GDD and the composite July/Aug GDD had associated  $r^2$  values of 9.2% and 0.8% respectively. There was also an interesting negative relationship between August GDD and white spruce ring width in Nain. The fitted linear model for white spruce ring width as a function of August GDD had an  $r^2$  of 15.8% along the negative slope.

As for eastern larch growing in Nain (Figure 4.3), the maximum predictive strength of the two mean temperature variables was 5.6% and 4.6% for June and July respectively. June GDD and June/July GDD variables were able to improve upon this predictive power, explaining 6.9% and 7.4% of the variance in the record of eastern larch ring width respectively. July GDD and July/Aug GDD were unsuccessful in surpassing the predictive strength of mean June temperature with  $r^2$  of 4.4% and 0.6% respectively. Once again with eastern larch, there was an observed negative relationship between August GDD and ring width. August GDD as a predictor of eastern larch ring width produced a linear model with an  $r^2$  of 8.8% along the negative slope.

Linear models representing the relationships between predictor variables and radial growth in Kamestastin had overall higher  $r^2$  values than their counterparts in Nain. For white spruce growing in Kamestastin (Figure 4.4), the temperature variables, mean June and mean July, were able to explain 13.9% and 9.4% of the variance in ring width over the length of the common record ( $n=59$ ) respectively. June GDD and June/July GDD were again able to surpass this level of predictive strength, each explaining 16.4% and 20.8% of the variance in the record of white spruce ring width respectively. July GDD and July/Aug GDD were less suited as predictor variables, explaining 9.5% and 4.3% of the variance in white spruce ring width respectively. In this case there was no significant relationship between August GDD and ring width with an  $r^2$  of only 0.1%.

The relationship between temperature and eastern larch ring width was quite strong, with values for  $r^2$  of 28.9% and 20.8% associated with mean June and mean July respectively (Figure 4.5). The predictive strength of June GDD and June/July GDD was higher, with associated  $r^2$  values of 35.4% and 46.9% respectively. Linear models with July GDD and July/Aug GDD as predictors of eastern larch ring width explained comparatively low amounts of variance, 22.7% and 4.3% respectively. August GDD

again had no significant control over ring width throughout the record, returning an associated  $r^2$  value of 0.3%.

#### ***4.6 Discussion***

The composite variable of June/July GDD, representing an accumulation of growing degree-days over the months of June and July, was an overall better predictor of radial-growth in northern Labrador than traditionally used monthly temperature variables (mean June and mean July). June/July GDD as a predictor variable was able to explain 46.9% of the variance in the record of eastern larch ring width from Kamestastin. This represents a significant increase in the predictive power of the linear model when compared with an analogous model constructed using mean June temperature as a predictor variable, which was able to explain a comparatively low 28.9% of the variance in eastern larch ring width.

The negative relationship between August GDD and radial growth in Nain suggests that an overall smaller growth ring would be produced by both white spruce and eastern larch during years in which daily mean temperature would reach high levels or remain high for an extended period of time during the month of August. This could be signaling some form of drought intolerance in both species.

Interestingly, no relationship was found between August GDD and radial growth in either of the species in Kamestastin. Previous studies have found that trees growing in coastal sites such as Nain are more sensitive to temperatures later in the growing season than those growing further inland (Payette, 2007; Kennedy, 2010; Dumaresq, 2011; Nishimura and Laroque, 2011). More recently it has been found, using intra-annual measures of stem radius, that while variations in stem size appear synchronous throughout much of the growing season, there is a deviation towards larger stem sizes nearer the end of the growing season in coastal Labrador (Chapter 3). Although these findings all point towards a later growing season in coastal Labrador, this hypothesis has yet to be fully understood.

Some of the findings from this study help to assess the overall suitability of both white spruce and eastern larch for dendrochronological research at high-latitudes. In both



white species, the series intercorrelation values were well above the threshold for significance, suggesting an overall synchronicity in tree growth at both sites (Table 4.1). The values for average mean sensitivity attributed to the white spruce chronologies were relatively low in this instance but were comparable to values found for white spruce at treeline in the Kennedy (2010) study (Appendix C). Both series intercorrelation and mean sensitivity were higher for eastern larch than they were for white spruce. During the regression analysis it became clear that eastern larch growing in inland Labrador near treeline are extremely sensitive to temperature variables, making it an excellent species for future dendroclimatological research. The strength of the relationship between June/July GDD and eastern larch ring-width, provides an interesting opportunity to possibly improve upon previous reconstructions of climate across the circumpolar boreal forest.

#### ***4.7 Conclusion***

An accumulation of GDD over the months of June and July was identified as an overall better predictor of radial growth than traditionally used mean monthly temperature variables in northern Labrador. By considering the predictive strength of this index variable, it would be possible to improve reconstructions of past climate and better our understanding of future tree growth under different climatic regimes. Additional work should be done to further refine the index of accumulated GDD so that it better encompasses the actual period over which temperature exerts its greatest influence on radial stem size. This period is likely linked with the phenology of ring development and would therefore vary across the landscape.

The large difference in predictive power between the two sites is explained by their overall location in reference to treeline. Kamestastin is located closer to treeline than Nain. While trees growing within the Nain site are inhabiting a continuous forest, trees in the Kamestastin area are pushed to the very edge of their range, opportunistically colonizing low lying areas in a heavily fragmented forest. The harsh temperature limited environment in Kamestastin cause trees here to be more sensitive to climate than their coastal counterparts, which have the benefit of coastal buffering to regulate extremes in temperature. Trees growing in sites like Kamestastin, at the very edge of their range,

should be targeted for future dendroclimatological study. Strong models can be built from the tight link between radial growth and climate in these harsh northern environments.

Elevated values for accumulated August GDD were found to negatively impact annual ring width in coastal Labrador, a relationship that was non-existent in trees growing further inland. We therefore hypothesize that there exists a drought intolerance in coastal conifers late in the growing season and that the growing season itself has an earlier end in inland locations.

Emphasis should be placed on the use of eastern larch in future dendroclimatological research at high latitudes. This species was found to be extremely sensitivity to environmental inputs and was heavily influenced by our composite June/July GDD variable. With more knowledge regarding the phenology of active ring formation in eastern larch and its association with temperature, this species could yield important information regarding past climate and the impacts of future climate in the boreal forest of eastern North America.

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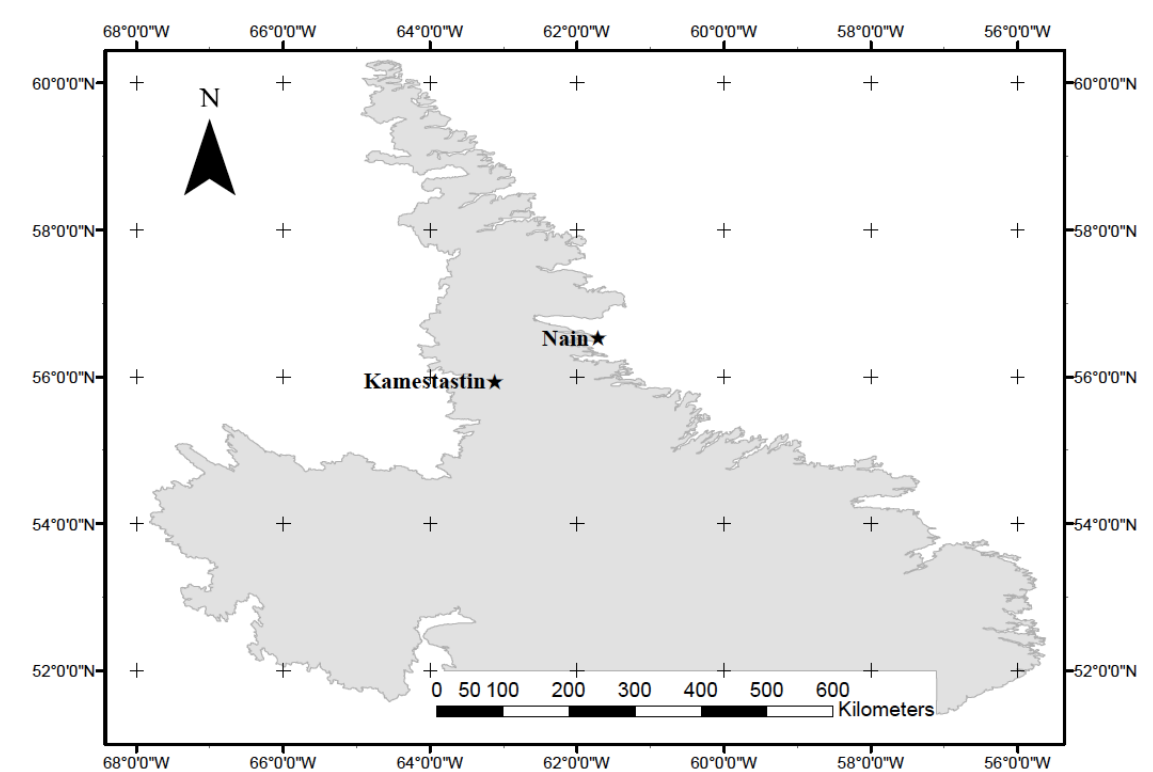
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#### 4.9 Tables and Figures

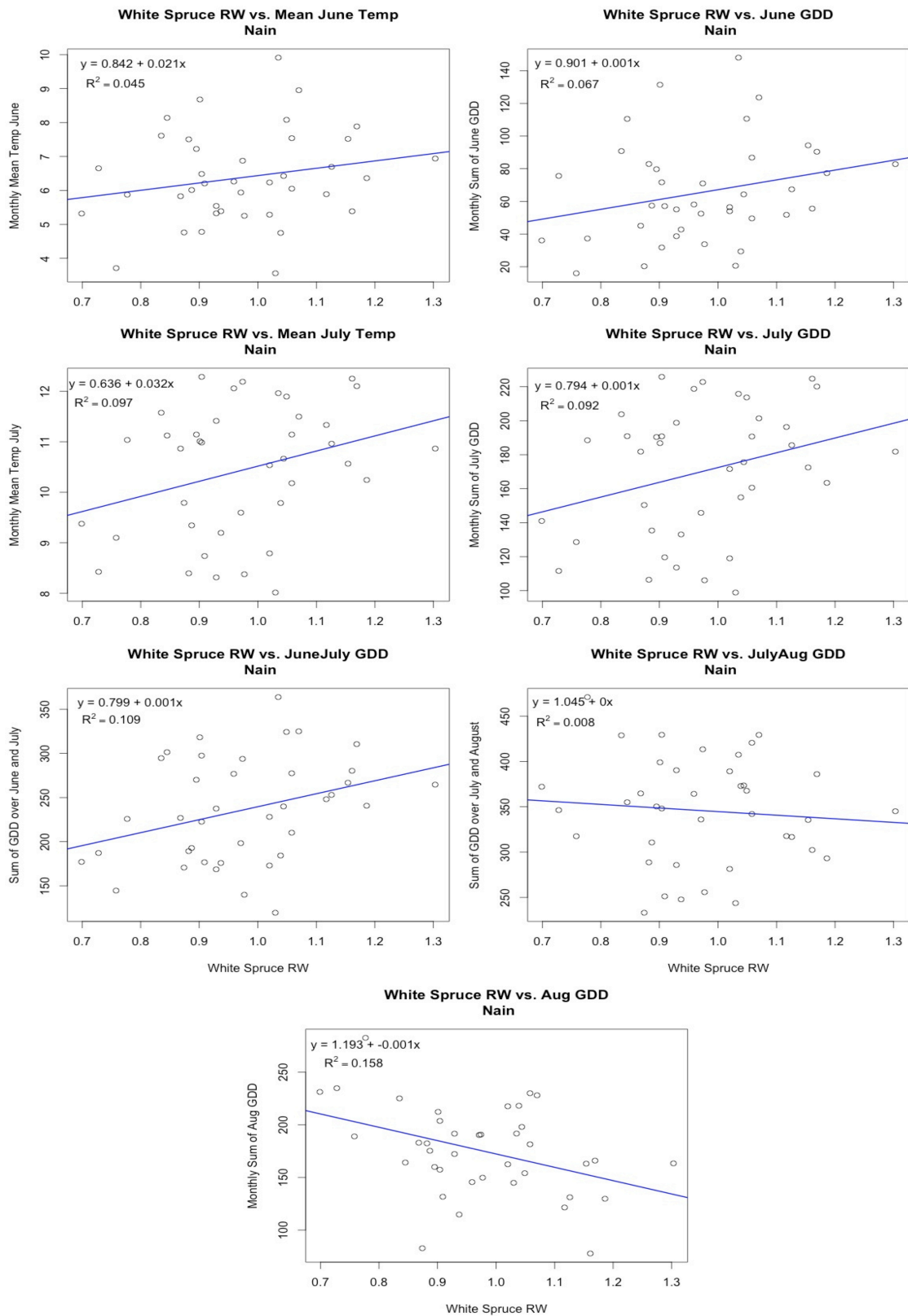
**Table 4.1:** Site and chronology information for the raw master chronologies. Chron. Length = Chronology length, Auto Corr. = Autocorrelation: indicates the effect of previous year's growing conditions on the current year's growth. AMS = Mean sensitivity: demonstrates mean year-to-year variability of radial growth within the chronology. MSI = Mean series intercorrelation: indicates the strength of the relationship between all samples taken from the same location using 30-year overlapping segments (values above 0.4225 are significant above the 99% confidence interval).

Site	Latitude	Longitude	Chron. Length	Avg. Age of Trees	Auto Corr.	AMS	MSI
WS-KAM	55°56'48.2"	63°07'17.3"	286 yrs.	104 yrs.	0.793	0.208	0.507
LA-KAM	=	=	129 yrs.	83 yrs	0.589	0.301	0.686
WS-NAIN	56°32'06.6"	61°43'23.4"	82 yrs.	65 yrs.	0.727	0.175	0.701
LA-NAIN	=	=	91 yrs.	60 yrs.	0.648	0.255	0.770

**Figure 4.1:** A map showing the location of the two study sites in Northern Labrador, Canada.

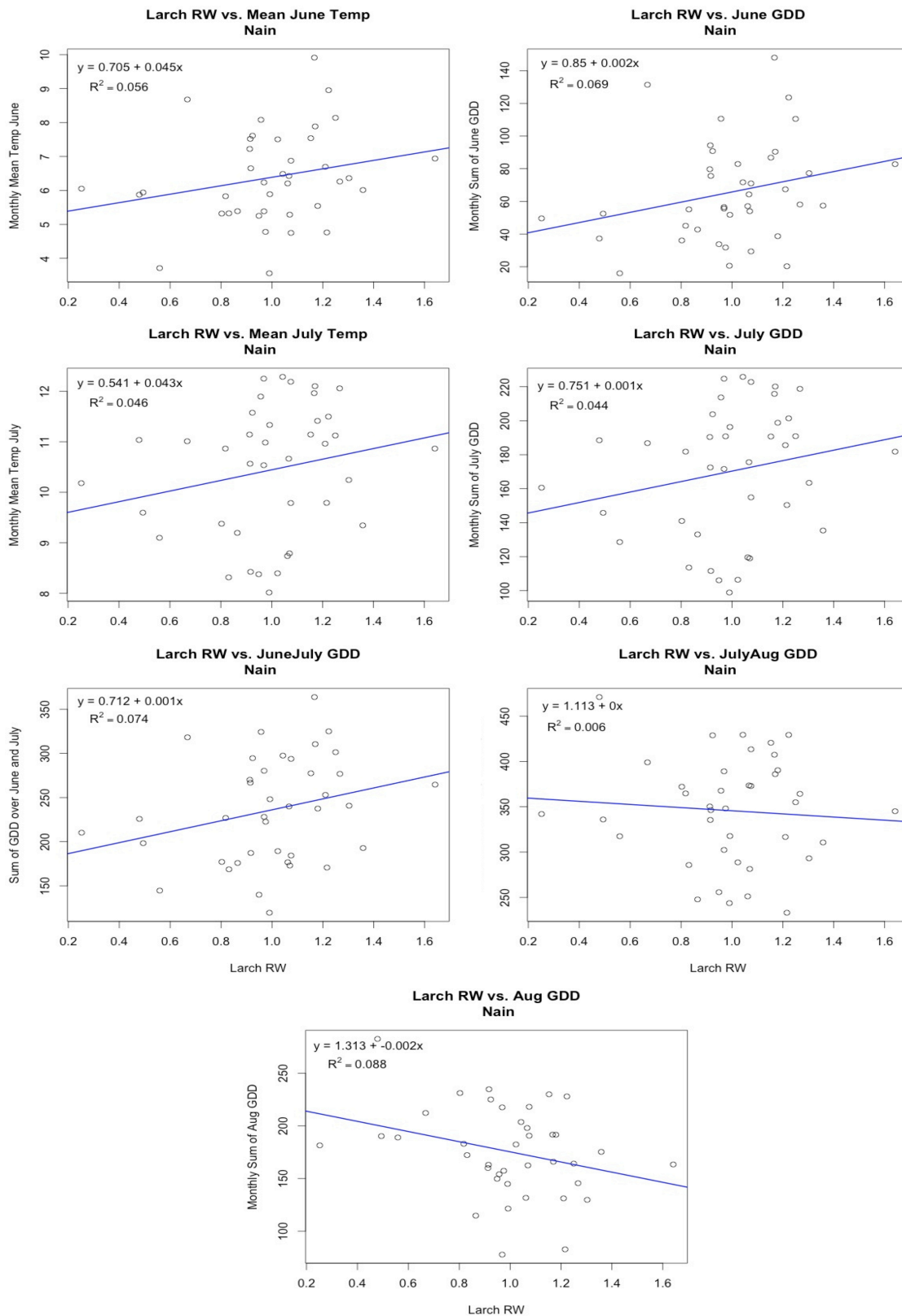


**Figure 4.2:** Linear models fitted to data of annual white spruce ring width in Nain as a function of different temperature driven climate variables (n=39 years).

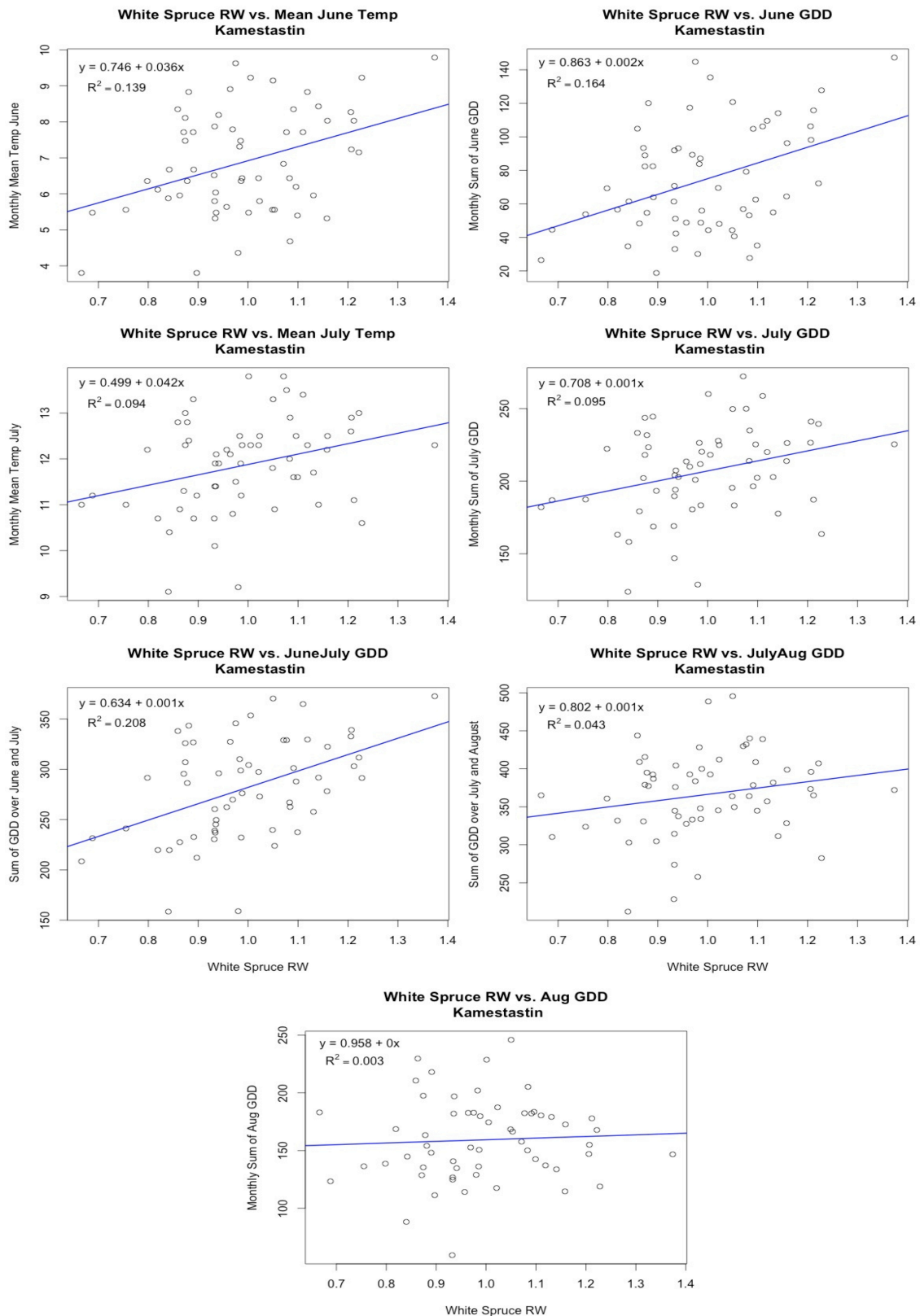




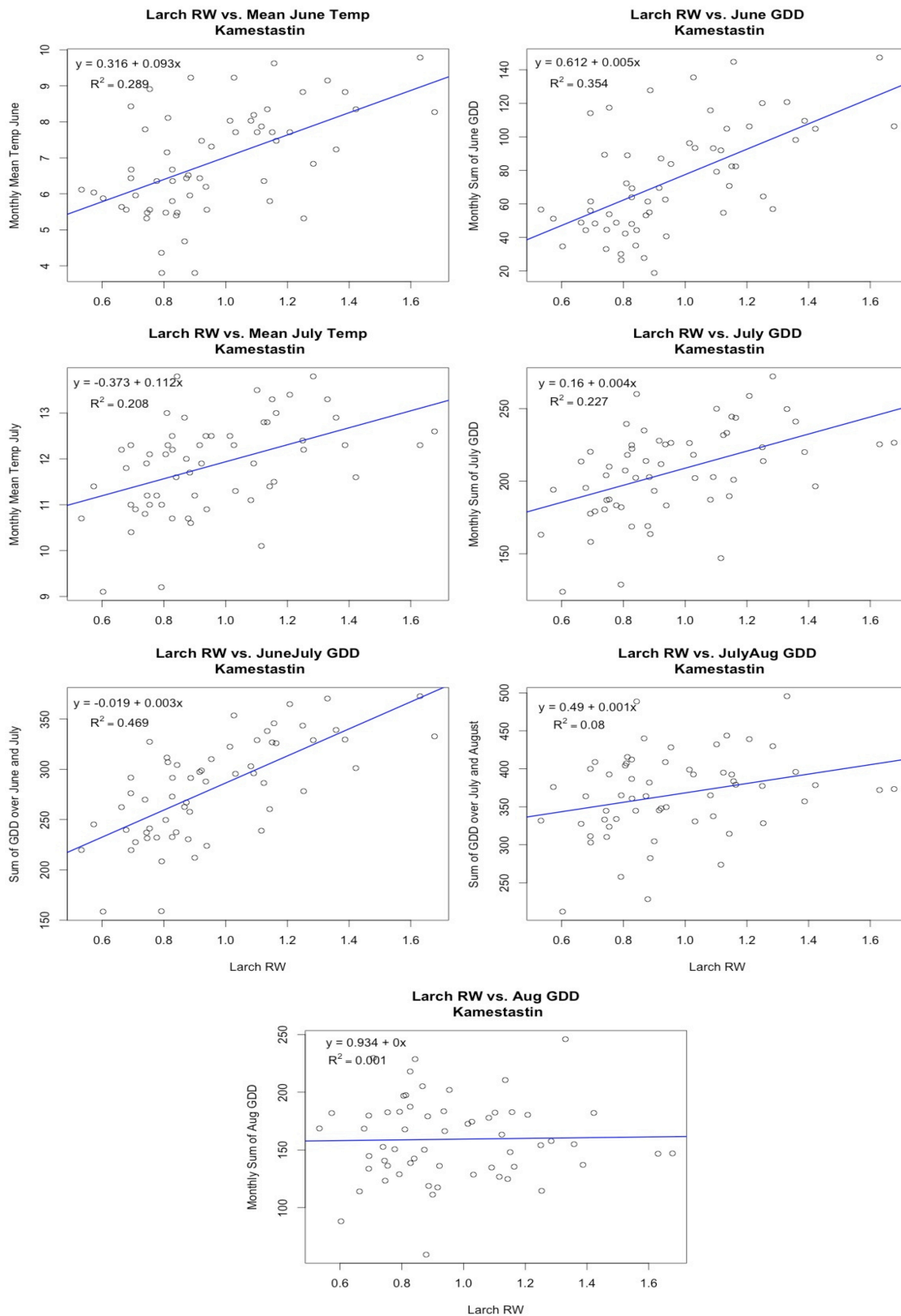
**Figure 4.3:** Linear models fitted to data of annual eastern larch ring width in Nain as a function of different temperature driven climate variables (n=39 years).



**Figure 4.4:** Linear models fitted to data of annual white spruce ring width in Kamestastin as a function of temperature driven climate variables (n=59 years).



**Figure 4.5:** Linear models fitted to data of annual eastern larch ring width in Kamestastin as a function of temperature driven climate variables (n=59 years).



## CHAPTER 5

### CONCLUSION

Historically, tree-ring research undertaken in Labrador has provided a general understanding of the dynamic radial growth-climate relationship across the landscape. The important questions raised during these investigations called for a creative and novel approach to hypothesis testing. High-resolution climate and radial growth data were collected for the first time in Labrador, providing a shift in focus and a new perspective from which to explore previously unanswered questions. The findings presented in this thesis provide a deeper understanding of the effect of temperature on the radial growth of conifers in the northern boreal forest of Labrador.

This study identifies the onset and cessation of white spruce radial growth during the growing season (Chapter 2). The direct view of tracheid cell development and active ring formation imparted by the micro-coring technique provided a means of delineating the phenology of white spruce radial growth in coastal Labrador. During the 2014 growing season, radial growth was initiated between June 23<sup>rd</sup> and 30<sup>th</sup>. The lignification of secondary cell walls began three weeks later between July 21<sup>st</sup> and 28<sup>th</sup>, signaling the near end to differentiation for the first tracheid cells to emerge from the vascular cambium. A transition to the production of latewood cells took place the following week, between July 28<sup>th</sup> and August 4<sup>th</sup>, four weeks after the initiation of radial growth. The end of tracheid cell production occurred eight weeks after initiation between August 20<sup>th</sup> and 25<sup>th</sup>.

This growth sequence occurred much later in the summer season than what was originally hypothesized, and begins to explain the differences found in tree-ring climate relationships by other researchers in Labrador. By having the trees still actively growing late into August, this helps to explain the late-summer/early-autumn climate relationships suggested by other researchers as being important, giving them a higher degree of viability. This new information is crucial if we are to understand the mechanics of ring development and its association with climate in an annual cycle of tree growth.

By understanding when the tracheid cells in Labrador were being produced, I then tried to determine the main climatic factors driving this cell radial growth with sub-monthly temporal resolution (Chapter 3). By focusing on this main period of radial growth, a connection was made between high-resolution records of stem radius change, as provided by circumference band dendrometers, and temperature variables on a daily scale. I found that radial stem size was driven primarily by minimum temperature on a daily scale, with an approximate one-week lag incorporated into the growth cycle. This observation brings to light the possible importance of a maintained threshold temperature needed for the initiation and progression of xylogenesis.

The idea of a possible minimum threshold temperature precipitated the further investigation of the climate/tree ring relationship in Labrador. Why are monthly means usually used for radial growth relationships, when my research indicates that the minimum threshold was the most important factor, and the trees then react to elevated ambient temperatures approximately 7 days later? This evidence provided an impetus to eliminate the classic mean monthly variables, and look more specifically at the threshold temperature, and then move the temporal scale from monthly to a daily scale. It led me directly to growing degree-days (GDD) as an index of accumulated heat above this hypothesized threshold temperature.

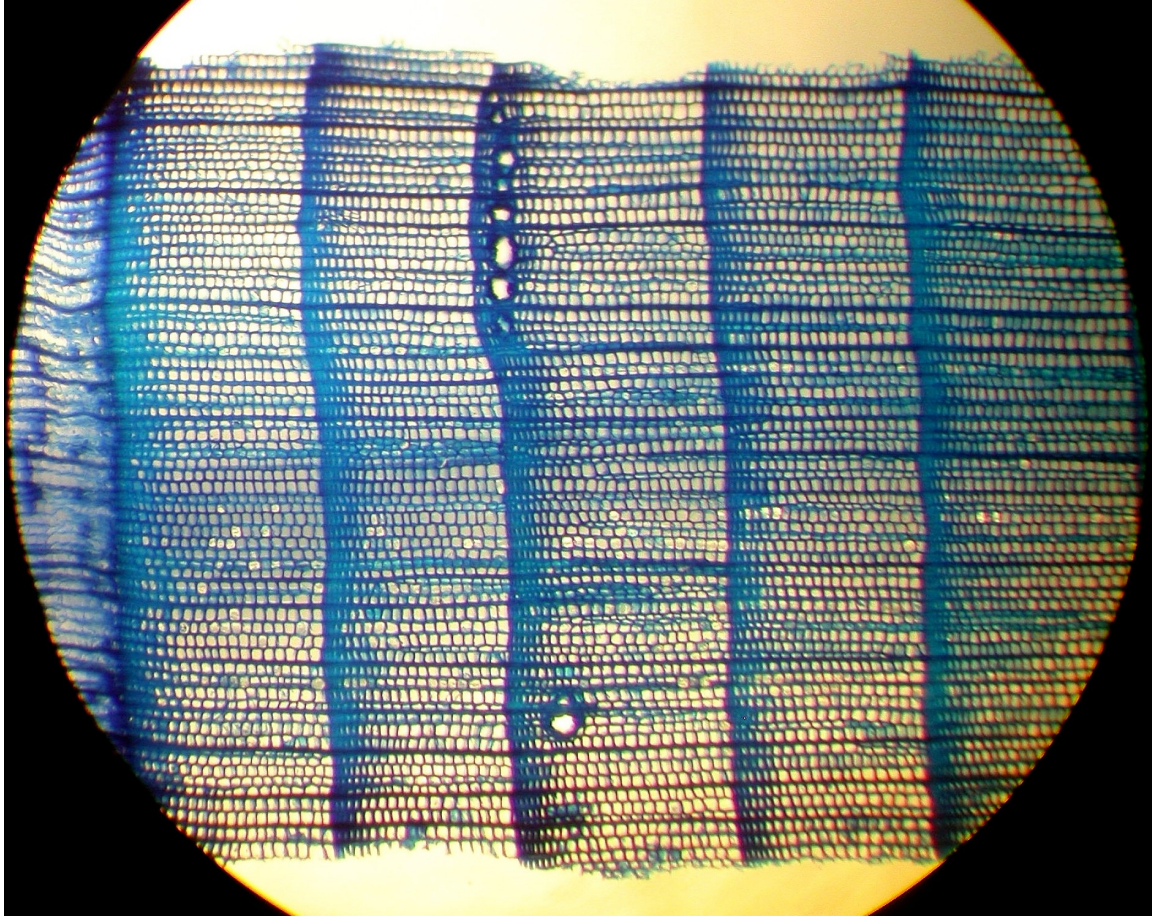
To assess whether the radial growth-climate relationship differs between inland and coastal study sites, I used GDDs to further examine the radial growth relationships at my two sites (Chapter 4). The ease of computation and the flexible nature of the GDD index allow it to be molded to fit the temperature and timescale requirements of a given research question. Linear regression analysis was used to compare the strength of accumulated GDD variables against that of commonly used mean-monthly temperature variables as predictors of annual ring width. A GDD index of accumulated heat over the months of June and July was identified as the best predictor of annual radial growth in northern Labrador. By considering the strength of the relationship between June/July GDD and annual ring width, it would be possible to create improved temperature reconstructions and better understand the effect of climate change on future tree growth at treeline in the northeastern boreal forest of North America.

The use of new techniques in answering dendroclimatological questions in Labrador allowed for a better understanding of the complex relationships between radial growth and climate. Additional work is needed in order to further refine the index of accumulated GDD so that it better encompasses the actual period over which temperature exerts its greatest influence on radial stem size. This period is linked with the phenology of ring development and would therefore vary across the landscape. These are important steps towards creating accurate predictions of boreal forest structure and extent as it changes due to a shift towards a warmer climate in the north. Such predictions can provide important information regarding the future role of the boreal forest in the global carbon cycle.



## APPENDIX A: STAINING PROTOCOLS

### *A.1 Toluidine Blue Single Staining Method*

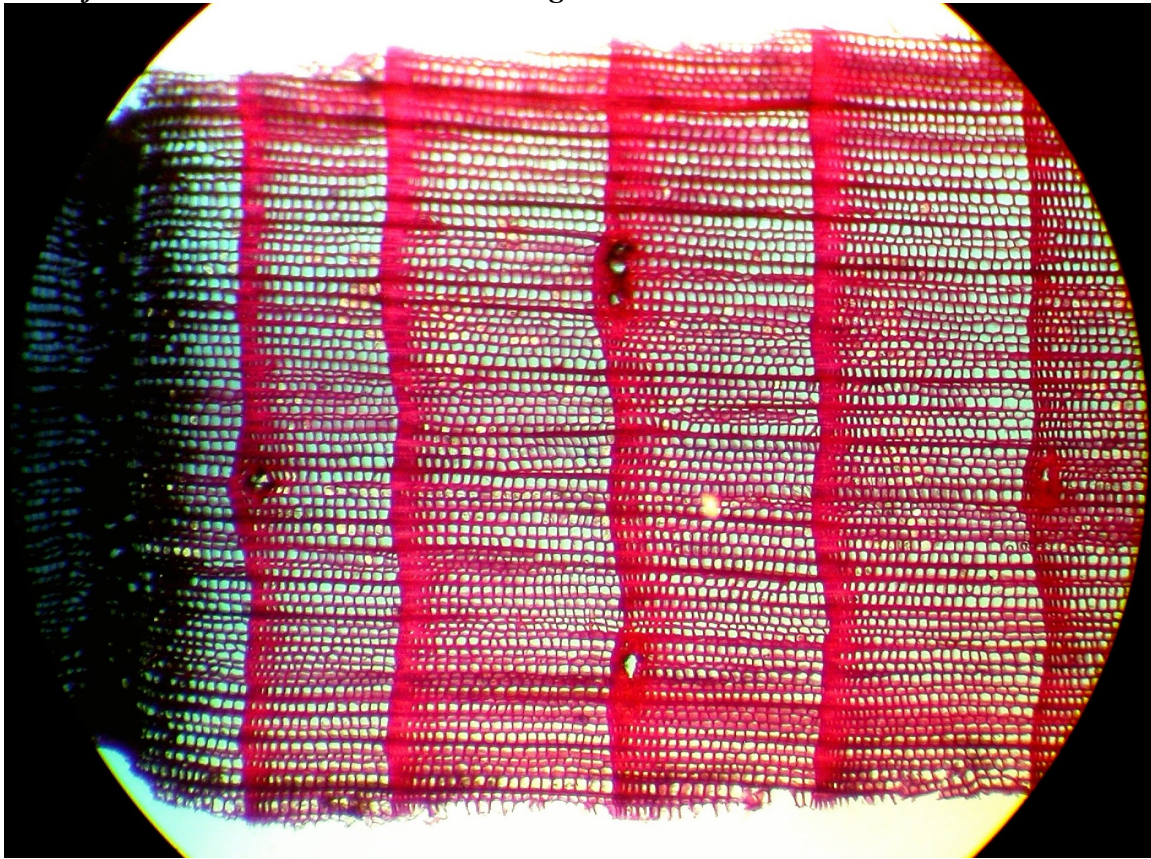


A solution of 0.1% toluidine blue and aqueous borax was used.

- 10  $\mu\text{m}$  thin sections were produced from microcores using a manual sliding microtome (GSL1).
- Transfer a small cross section to a glass slide and keep moist with a few drops of distilled water.
- When ready for staining, rinse the small section several times by pumping distilled water through it while holding it to the slide using the tip of a pipette.
- Dry the area around the thin section using a paper towel, leaving the glass slide and sample as dry as possible before applying the stain.
- Place a few drops of the aqueous toluidine blue/borax stain directly over top of the sample, enough to cause it to “swim” in the staining solution.
- Leave the sample to absorb the stain undisturbed for 30 minutes.
- Rinse the thin section in the same way as before, pumping distilled water through the sample on the slide using a pipette. Repeat this several times until the excess water runs clear.
- Place a few drops of glycerin or glycerin solution on top of the now stained section before carefully applying a cover glass to avoid trapping bubbles.



### *A.2 Safranin / Fast Green Double Staining Method*



0.2% aqueous solutions of both Safranin O and Fast Green were used.

- 10  $\mu\text{m}$  thin sections were produced from microcores using a manual sliding microtome (GSL1).
- Transfer a small cross section to a glass slide and keep moist with a few drops of distilled water.
- When ready for staining, rinse the small section several times by pumping distilled water through it while holding it to the slide using the tip of a pipette.
- Dry the area around the thin section using a paper towel, leaving the glass slide and sample as dry as possible before applying the stain.
- Place a few drops of the aqueous Safranin stain directly over top of the sample, enough to cause it to “swim” in the staining solution.
- Leave the sample to absorb the stain undisturbed for 10 minutes.
- Rinse the thin section in the same way as before, pumping distilled water through the sample on the slide using a pipette. Repeat this several times until the excess water runs clear.
- Repeat the last four steps, this time applying the aqueous Fast Green solution and leave the sample to absorb the stain undisturbed for 20 minutes this time.
- Thoroughly rinse the thin section in the same way as before.
- Place a few drops of glycerin or glycerin solution on top of the now stained section before carefully applying a cover glass to avoid trapping bubbles.



## APPENDIX B: REGRESSION ANALYSIS OF HOURLY TEMPERATURE BETWEEN SCHEFFERVILLE AND KAMESTASTIN

**Table B.1:** Linear regression equations representing the monthly relationship between Kamestastin (y) and Schefferville (x) with associated r-squared and standard error.

Regression Analysis	Equation	R-squared	Res. std. error
<b>Full year (2013-2014)</b>	$Y = -0.941 + 0.919x$	0.928	3.735
<b>Jul-13</b>	$Y = -0.252 + 0.940x$	0.677	2.946
<b>Aug-13</b>	$Y = -0.335 + 0.928x$	0.667	2.942
<b>Sep-13</b>	$Y = 0.697 + 0.813x$	0.705	2.716
<b>Oct-13</b>	$Y = 0.459 + 0.872x$	0.789	2.297
<b>Nov-13</b>	$Y = -1.484 + 0.689x$	0.608	3.420
<b>Dec-13</b>	$Y = -2.410 + 0.807x$	0.786	2.942
<b>Jan-14</b>	$Y = -4.176 + 0.791x$	0.675	4.595
<b>Feb-14</b>	$Y = -9.717 + 0.616x$	0.525	3.823
<b>Mar-14</b>	$Y = -6.837 + 0.666x$	0.610	4.046
<b>Apr-14</b>	$Y = -3.134 + 0.809x$	0.615	3.776
<b>May-14</b>	$Y = -2.442 + 0.957x$	0.809	2.500
<b>Jun-14</b>	$Y = -0.268 + 0.798x$	0.480	4.037

Very strong  $r^2$  values were associated with the linear models fitted to the hourly temperature variables from Kamestastin as a function of hourly temperature at Schefferville (Table B.1). The strongest  $r^2$  value belonged to the linear model fitted to the complete dataset before they were broken down into monthly intervals. The fitted linear model explained 92.8% of the variability in the year long dataset. After being broken down, linear models fitted to each month long set of temperature observations, Kamestastin temperature as a function of temperature at Schefferville, explained between 48.0% and 80.9% of the variability between the fitted model and the observed instrumental data.

The elevated  $r^2$  values associated with the linear models provide confidence in the extrapolated long-term temperature dataset for Kamestastin. The lowest  $r^2$  value that was returned was 48%, associated with the linear model fit to the temperature data from the month of June 2014 (Table B.1). The reason that the predictive power of this model is lower than the others is due to the size of the dataset in June. Issues with the climate station at Kamestastin caused the temperature record to be cut short. This record contains only about 12 days of data. Beyond the June dataset, only one other month returned an  $r^2$  value below 60%. The linear model fit to the temperature data from February 2014 could only account for 52.5% of the variability.

## APPENDIX C: STUDY SITE VALIDATION

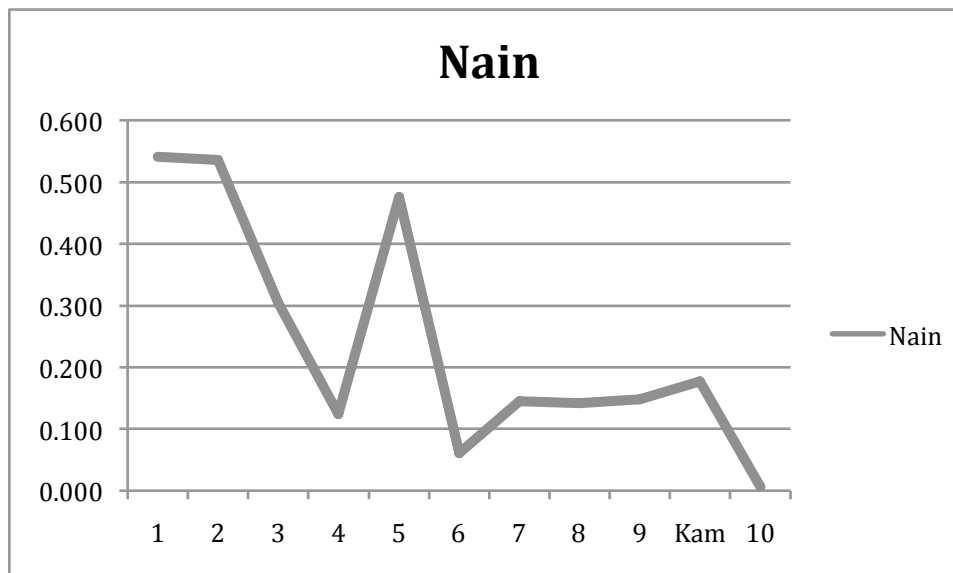
A correlation matrix was built, comparing the two new white spruce sets in this study to ten existing white spruce sets extracted from an array of sites located along treeline in northern Labrador (Table C.1). These additional sites were sampled in 2009 for a study completed by Chris Kennedy (Kennedy, 2010). In the matrix, a common time interval shared by all chronologies was used (n=82 years). The Pearson's product moment correlation coefficient statistic was used to compare each new set of standardized residual ARSTAN chronologies to the ten old, to determine whether tree growth within this study follows radial tree growth at any of the Kennedy (2010) treeline sites.

**Table C.1:** Pearson's product moment correlation matrix comparing the two study sites of Nain and Kamestastin to the ten previously sampled by Kennedy (2010).

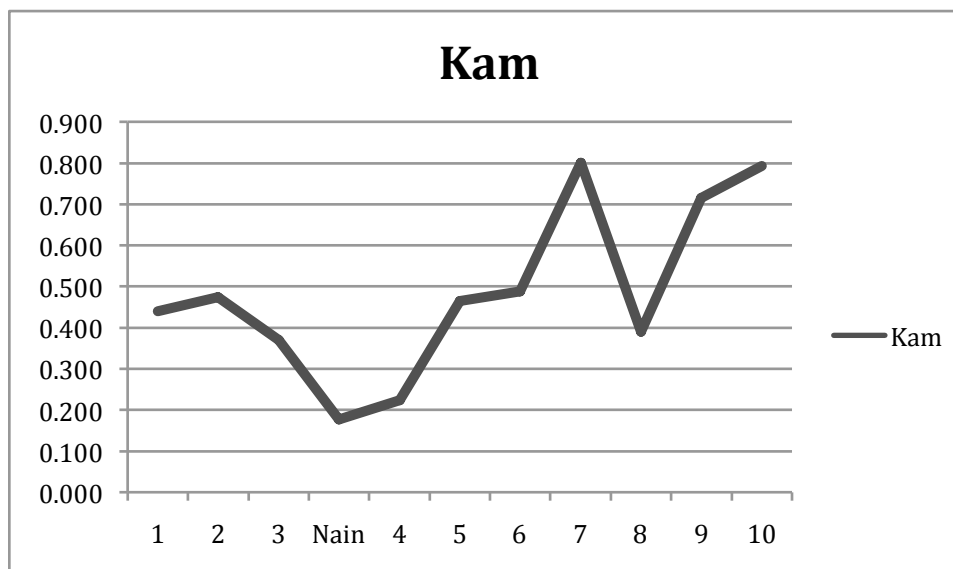
	1	2	3	Nain	4	5	6	7	8	9	Kam	10
1	--											
2	0.775	--										
3	0.608	0.695	--									
Nain	0.541	0.536	0.305	--								
4	0.538	0.497	0.750	0.124	--							
5	0.610	0.712	0.703	0.476	0.444	--						
6	0.608	0.523	0.580	0.060	0.701	0.539	--					
7	0.587	0.535	0.621	0.145	0.526	0.596	0.719	--				
8	0.537	0.607	0.699	0.142	0.746	0.492	0.678	0.633	--			
9	0.608	0.705	0.654	0.148	0.560	0.546	0.699	0.850	0.693	--		
Kam	0.439	0.474	0.370	0.177	0.224	0.465	0.488	0.802	0.390	0.715	--	
10	0.484	0.606	0.504	0.006	0.436	0.431	0.658	0.820	0.589	0.880	0.794	--

The white spruce correlation analysis is able to illustrate how these two study sites fit into the regional picture of radial-tree growth from the previous study by Kennedy (2010). Trees growing at the Nain sample site shared the most commonality with those growing within coastal areas north of Nain (sites 1 and 2 from the Kennedy (2010) study; see Figures C.1 and C.2). White spruce from the Mistastin Lake site seem to be growing more similarly to white spruce that has colonized inland sites nearest itself, labeled 7, 9, and 10 in the Kennedy (2010) study (Figure C.3).

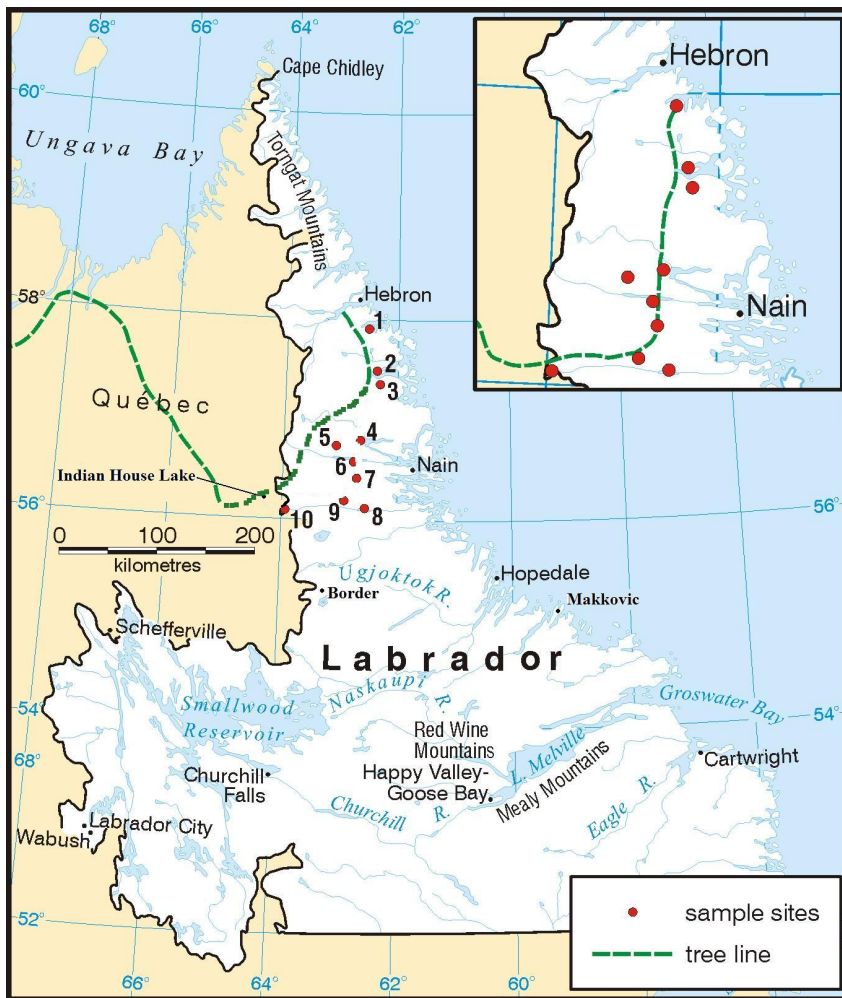
**Figure C.1 :** Level of correlation between the Nain study site and each other site.



**Figure C.2 :** Level of correlation between the Kamestastin study site and each other site.



**Figure C.3 :** Study site map from the Kennedy study (Kennedy, 2010).



The correlation analysis allows for the two study sites considered in this paper to be fit in to the greater picture of white spruce growth along treeline sites across all of Labrador. Since it was found that the white spruce growing in Nain is most representative of tree growth along the northern coast, and that the white spruce growing near Mistastin Lake is displaying a similar growth signal to that of the trees growing inland, it can now be said with a certain level of confidence that our two sites are independently representative of each of these wider bioclimatic zones and are suitable for comparative type study.

## APPENDIX D: DENDROCLIM CORRELATION FUNCTION ANALYSIS

Monthly records of mean temperature were established for both Kamestastin and Nain during the regression analysis outlined in Chapter 4 and Appendix B. These were used as an input for the program DendroClim2002 (Biondi and Waikul, 2004), which helped to evaluate the strength of the relationship between each monthly temperature variable and site-specific chronologies for both white spruce and eastern larch. A time interval of April from the previous growth year to September of the current growth year was chosen since this period contains two full growing seasons and would provide a good picture of the radial growth/climate relationship (Table D.1).

**Table D.1:** Results from the DendroClim analysis. Shaded grey cells represent correlations that are above the 95% threshold of a bootstrapped confidence interval.

year n-1	APR T	MAY T	JUN T	JUL T	AUG T	SEP T	OCT T	NOV T	DEC T
WSKAM	0.3471	0.2010	-0.0545	-0.1762	-0.1118	0.0378	0.1840	0.0604	-0.1015
LAKAM	0.3003	0.2395	0.2151	0.2410	0.0743	0.0367	0.2338	0.1312	-0.0938
WSNAIN	-0.0720	0.0323	-0.1906	-0.1738	-0.1035	-0.2516	-0.0328	0.0131	-0.2349
LANAIN	0.1196	0.2688	-0.1006	-0.0249	0.0545	0.0530	0.0682	0.0192	-0.0746
year n	Jan T	Feb T	Mar T	Apr T	May T	Jun T	Jul T	Aug T	Sep T
WSKAM	-0.2454	-0.1581	-0.1040	-0.0936	0.0074	0.3705	0.3109	0.0466	0.1270
LAKAM	-0.0468	0.0311	-0.1498	-0.0893	0.1201	0.5320	0.4436	-0.0025	0.0815
WSNAIN	-0.1561	0.1770	-0.1630	-0.2290	-0.1401	0.2468	0.1423	-0.2478	-0.1373
LANAIN	-0.0565	0.1034	-0.0639	-0.0415	-0.0670	0.2926	0.2272	-0.0884	0.0054

The DendroClim response function analysis revealed multiple connections between radial-growth and temperature. There were 15 monthly temperature variables that returned statistically significant values above the 95% confidence level, almost half of which were from the previous growing season (year = n-1) (see Table D.1). The seven temperature variables from the previous growing season that crossed the threshold for significance are more or less random with only a single instance where a monthly temperature variable was repeated. Both white spruce and eastern larch growing within

the Mistastin Lake site are significantly and positively influenced by warm April temperature from the previous growing season (year  $n-1$ ). The remaining eight statistically significant associations between tree growth and climate were with temperature variables from the current growing season (year  $n$ ). All four radial-growth chronologies have a positive relationship with warm June temperature. Elevated temperatures in July also lead to a wider ring in all but one of the sets; white spruce in Nain was the only unrepresented group in this case.

This is not the first observation of a link between summer temperature and tree growth in Labrador (Payette, 2007; Kennedy, 2010; Dumaresq, 2011; Nishimura and Laroque, 2011; Trindade et al., 2011; Kershaw and Laroque, 2012), or on a broader scale, tree growth within the circumpolar north (Cropper and Fritts, 1981; D'arrigo et al., 1992; Briffa et al., 1994; Kirdyanov et al., 2003; Levanič and Eggertsson, 2008). It has also been suggested that there may be a phenological shift and an increased importance of temperature from earlier in the growing season as one travels inland from the coast (Payette, 2007; Kennedy, 2010; Dumaresq, 2011; Nishimura and Laroque, 2011). For example, Nishimura and Laroque, (2011) describe a shifting relationship along a longitudinal gradient; in general, as one travels west, the importance of July temperature weakens while temperature during the spring months (May / June) become increasingly important. Here, we find that both white spruce and eastern larch growing within the Mistastin Lake site, our inland sample location, have a significant positive relationship with April temperature from the previous growing season (year  $n-1$ ), a relationship that is completely unrepresented within trees growing at our coastal site in Nain. This provides further evidence and strengthens the idea of a possible phenological shift along a longitudinal gradient in Northern Labrador.

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